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The stock of herring in the North Sea, and changes due to fishing

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PART I

The unity of the Downs herring stock, and its degree of mixing with other stocks in the northern and central North Sea

D. H. Cushing

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1. INTRODUCTION

In this paper the Downs stock is defined as that stock spawning in the Southern Bight of the North Sea and eastern English Channel in November and December. From the homogeneity of the vital population parameters within the Southern Bight fisheries, it will be concluded that as a stock of adults returning to their ground of first spawning (Burd and Cushing, 1962) the Downs stock is a unit stock.

There are three major spawning seasons for the North Sea autumn-spawning herring: in August and September off the Buchan coast of north-east Scotland, in September and October in the area of the Dogger Bank, and in November and December in the Southern Bight. It is possible that the Buchan and Dogger spawners (which were grouped as the Bank stock by Cushing and Burd, 1957) are distinct unit stocks like the Downs stock. The recruitment to each of the three spawning groups will be estimated, and the lack of correlation between recruitments to the spawning groups will be shown in the data up to 1960.

It has been known for a long time that fish of the Downs stock penetrate the northern and central North Sea during the summer feeding season. An attempt will be made to estimate the proportion of Downs fish on the feeding grounds during the summer.

2. THE UNITY OF THE STOCK EXPLOITED BY THE FISHERIES IN THE SOUTHERN BIGHT OF THE NORTH SEA

In October and November herring in maturity stages IV, IV/V and V are caught by drift nets all over the Southern Bight of the North Sea. The fishery moves southward and the younger fish appear to do so earlier than the older (Hodgson, 1939). A fishery for spawning fish starts in November on a few restricted grounds, continuing into December and January in the area between the Galloper L.V. and the Pointe d'Ailly; the fishery starts early at the Galloper and ends late at Ailly, as if the apparent southward migration into the Southern Bight were continued into the Eastern Channel. From December to February, spent fish are caught off the French, Belgian and Dutch coasts; the fishery moves northward in time as if the spent fish were migrating back into the North Sea. In the 1920s, a spring fishery for spent herring took place from Lowestoft in late February, March and April (Hodgson, 1957); the fishery started off the Dutch coast, moved from the Brown Ridges towards the Indefatigable Bank and then towards the Silver Pit (Bolster, 1955). The simple view of this history of continuous and contiguous fisheries is of a migration of herring southward to spawn as far south as Ailly and a return migration of the spent fish into the North Sea.

The stock moving into the Southern Bight fisheries could be considered as a single population, a group of populations, or a population which accepts immigrants or yields emigrants. Hodgson (1929) showed that l_1 distributions of adults from the East Anglian fishery had three modes, which might be linked with three spawning seasons (summer, autumn and winter, or Buchan, Dogger and Downs). However, Cushing (in Burd and Cushing, 1962) has shown that such l_1 distributions could be generated in the recruitment mechanisms; Burd (Burd and Cushing, 1962) has shown that the l_1 distributions within a year-class in the East Anglian fishery remain the same from recruitment to extinction. Because the means of the l_1 distributions in the Buchan and Dogger spawning fisheries are larger than those of the Downs fisheries, extensive adult mixing should have the effect of radically changing the l_1 distributions from year to year within a year-class. Cushing (1958a) showed that the vertebral counts in the East Anglian fishery vary less within year-classes than within age groups; with the l_1 evidence this suggests that the adult year-classes retain their identity from recruitment to extinction. Because of the larger l_1s in Buchan and Dogger, any mixture in the East Anglian fishery should be seen in an increase in the magnitude of l_1 with age. Burd (Burd and Cushing, 1962) has shown that this does not occur. Hodgson (1929) wrote in his conclusion to a considerable body of work:

'The age and length records taken during a period of six years show that the stock of herrings in the western part of the southern North Sea may be considered to be a definite unit in the herring population of the North Sea as a whole. The age determinations point to a return each year of the old stock of fish, and from the similarity of the outline of the figures representing the older year-classes, and the regular increase in size, and gradual elimination of the length groups from year to year, it may be inferred that there have been no outstanding additions of fish from other areas where the length at a given age was different from that of the southern North Sea; neither, apparently, has there been any noticeable migration from the stock.' For rather different reasons, this represents our present view. Hence it is likely that the adult year-classes retain their identity from year to year. This indeed was the real basis of Hodgson's successful method of forecasting (1932), based on the statement quoted above.

In his extensive study of the French herring fisheries based on Boulogne in the late autumn and winter, Le Gall (1935) found three groups of fish, Sandettié, Nord Somme and Ailly. No differences between them were established from a large number of biometric measurements, with the exception of small and consistent differences in vertebral sum. For a period of years percentage age distributions were given for each of the three fisheries, Sandettié, Nord Somme and Ailly, and they are very much alike. As the three groups are of herring spawning at very nearly the same season, the congruence of age distributions would imply that recruitment and mortality were similar in the three groups. The inference remains true even if the three groups were really separate and self-sustaining stocks; from the point of view of management, the three postulated stocks possessed identical parameters of recruitment, growth and mortality, and could be treated as a unit for management purposes.

In Cushing and Burd (1957), it was shown that both before and after the second World War, age distributions from Boulogne, Ostend and East Anglia were similar. In contrast, these age distributions differed from those on the Dogger both before the first World War and after the second; between the wars, the mortality rates were rather alike, but although certain year-classes were common to the two groups of fisheries, Dogger and Southern Bight, some others were markedly different. A spatial difference in the relative abundance of year-classes is not in itself evidence of stock separation, because older and younger fish in a stock may live in different areas. But the Dogger fishery is partly a spawning fishery, as is that at Sandettié and Boulogne; the age distributions in the Southern Bight are congruent with those at Sandettié and Boulogne, but not with those on the Dogger. With these facts in mind, the contrast between the age distributions from the Dogger and those from the Southern Bight suggests a separation in stocks, whereas the correspondence between the three fisheries in the Southern Bight which also exploit spawning herring suggests a single stock.

A stock is defined in this limited way as a population of adult fish in which mortality, growth and recruitment amongst the adult year-classes are the same in all fisheries sampled.

To test whether two fisheries are exploiting the same or different stocks, a regression is formed by plotting the percentage of the catch in a given age group for a given year in one fishery on that for the same age group and the same year in another fishery. Differences between these percentage age compositions of fully recruited fish are due partly to year-class differences, but in the main to mortality, and so, if we plot the percentages by age and year in one fishery on the percentages by age and year in another, differences in mortality are being compared. If the mortality in the two fisheries is the same, the slope is a bisector, passing through the origin, i.e. the proportionate decrease from age to age within a year and from year to year (whatever the changes in the magnitude of mortality) is the same. So the bisector test is a sufficient one for the homogeneity of total mortality in the two fisheries. Regressions of this kind for the fisheries of East Anglia and Boulogne, and for East Anglia and the Belgian spent herring fishery, are shown in Figures 1 and 2.

Year-class differences between the stocks being compared in this way increase the variance of the regression of percentages in one fishery on those in another; a succession of more than two good year-classes in one fishery only would bias the regression (to a curve above the bisector in younger age groups and below it in older ones) until these year-classes were extinguished or a new level of recruitment was established. So if the points are scattered evenly about the regression, with no obvious bias or curvilinearity, it is likely that mortality is of the same magnitude in the two fisheries and that the succession of two or more abnormal year-classes was common to both fisheries. The crude recruitment to the East Anglian fishery from 1925–58 shows no upward or downward trend; from 1933–5 and from 1951–5 there are successions of poor year-classes (see Figure 7, below). It will be shown that they do not bias the regressions, implying that the year-classes are common to the stocks examined. Other evidence on this point will be produced below.

If the slope of the regression is not that of the bisector, the total mortalities in the two fisheries are not the same. By a modification of the technique, the magnitudes of the mortalities in the two fisheries can be compared. Consider the line joining the two points given by successive ages of the same year-class in fisheries x and y, with no year-class variation, where x_1 and y_1 are percentages of a given age and x_2 and y_2 are percentages of the subsequent age. On an arithmetic scale the slope is $y_1 - y_2/x_1 - x_2$; if plotted in logs the slope is

$$\frac{lny_1 - lny_2}{lnx_1 - lnx_2},$$

which is the mortality ratio, Z_y/Z_x. When $Z_y/Z_x = 1$,

$$\frac{lny_1 - lny_2}{lnx_1 - lnx_2} \left\{ = \frac{y_1/y_2}{x_1/x_2} \right\} = \frac{y_1 - y_2}{x_1 - x_2} = 1;$$

this justifies the bisector relationship described above. With a large amount of data, year-class variation appears as scatter about the bisector. When $Zy \neq Zx$, $\frac{y_1 - y_2}{x_1 - x_2}$ differs from $\frac{y_2 - y_3}{x_2 - x_3}$, necessarily yielding a curvilinear relationship in percentage distributions (I am grateful to Professor A. Bückmann for making this point to me); but $\frac{lny_n - lny_{n-1}}{lnx_n - lnx_{n-1}}$ is constant. The equation for such a regression is $\log y = \log a + b \log x$. The intersect on the ordinate includes that proportion (in logs) of older fish which do not contribute to the regression; for example, if the mortality ratio Z_y/Z_x is high some older fish will appear in the percentage age distribution with the low mortality rate but not in that with the high one. If a significant intersect is found on the arithmetic plot, it means that the data must contain an element of curvilinearity, i.e. $Z_y \neq Z_x$.

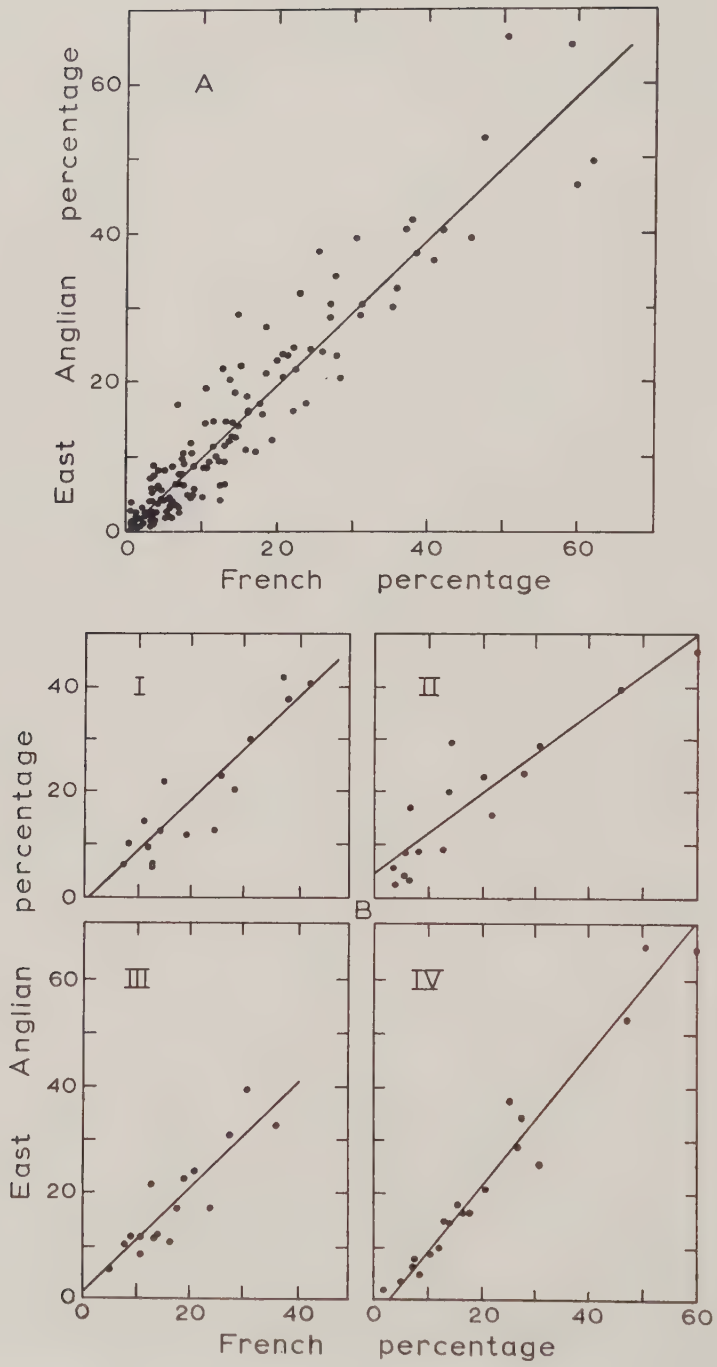

Fig. 1. A. *The relationship between the percentage of each age at East Anglia on the corresponding percentage in the same year at Boulogne from* 1926 *to* 1957, *for all ages. The regression is not significantly different from the bisector.*

B. *The same material as in Figure* 1*A, split into four periods for the younger age groups: I, four- to seven-year-olds,* 1926–9*; II, four- to seven-year olds,* 1934–7*; III, four- to seven-year-olds,* 1946–50 *excluding* 1948*; IV, three- to six-year-olds,* 1952–7, *excluding* 1954. *The regression for the period* 1934–7 *is significantly different from the bisector* ($p<0{\cdot}01$) *as is that for the period* 1952–7 ($p<0{\cdot}01$).

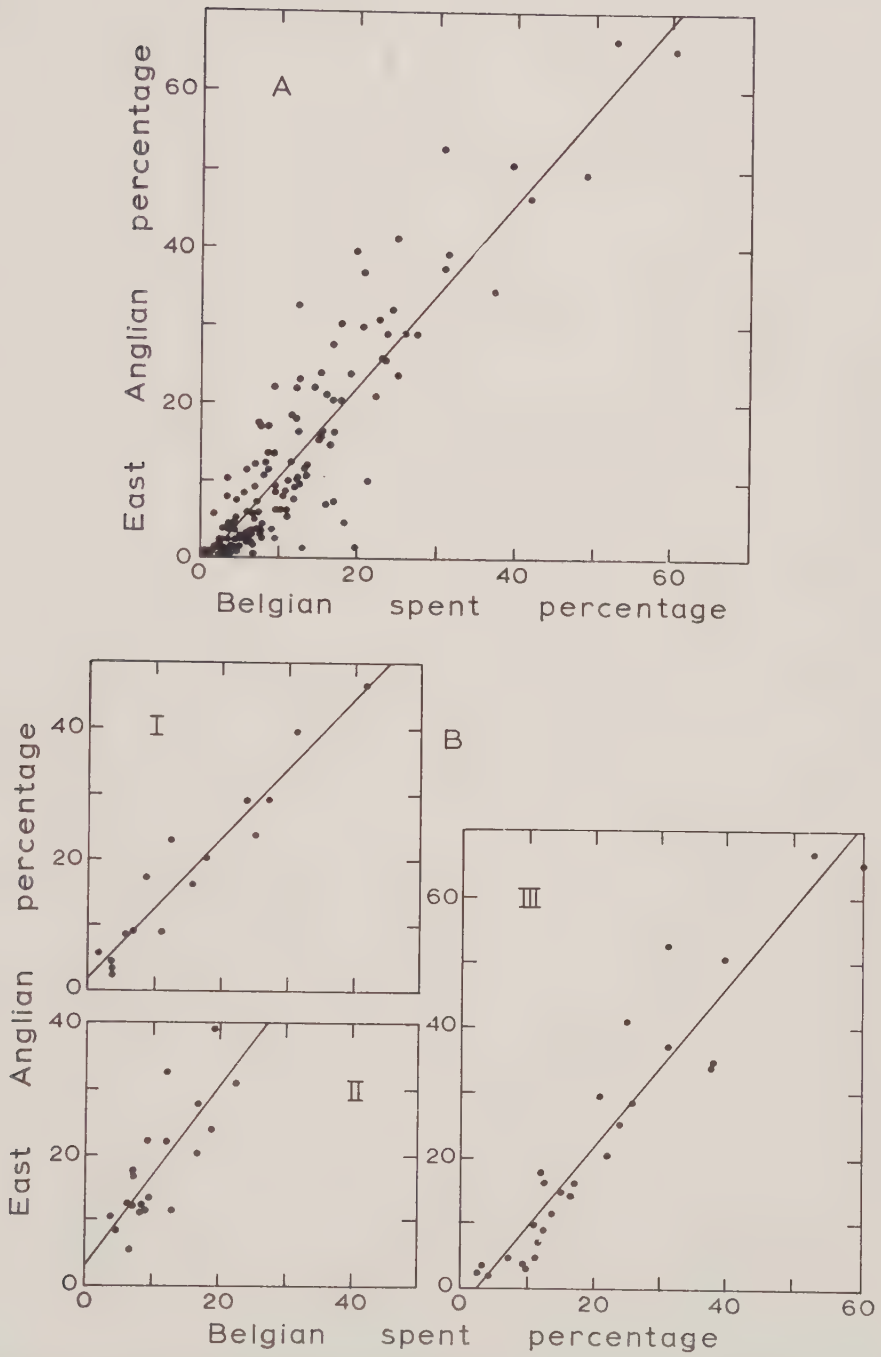

Fig. 2. A. *The relationship between the percentage of each age at East Anglia on the corresponding percentage in the same year in the Belgian spent herring fishery from* 1930–58, *for all ages. The regression is significantly different from the bisector* ($p<0{\cdot}01$). B. *The same material as in Figure 2A, split into three periods for the younger age groups: I,* 1934–7; *II,* 1946–50; *III,* 1952–8. *The regression for the last period is significantly different from the bisector.*

Available data include percentage age distributions (from three to nine or ten years of age) from the German Dogger fishery (Krefft, Schubert and Sahrhage, 1955), the English East Anglian fishery, the French Channel fishery (Le Gall, 1935; Ancellin, 1953) and the Belgian spent herring fishery (Gilis, 1958) for a period from about 1926 or 1930 to about 1958, with some gaps in the series. Provided that the stock in each fishery is adequately sampled, year-to-year changes in vulnerability can be ignored when percentage age distributions are being used.

Figure 1A shows the relationship between the percentage of a given age at East Anglia and that at Boulogne in the same year, e.g. the percentage of four-year-old fish at East Anglia is plotted against the percentage of four-year-olds at Boulogne in the same year; similarly for other age groups and other years. This is a clear relationship, which is not significantly different from the bisector, from which it may be concluded that the total mortalities in the two fisheries were the same from 1926–57 (excluding the war years). Further, the two series of poor year-classes referred to above have not biased the regression. Given that mortality was common, then it is likely that the poor year-classes were also common to the two fisheries.

The period was split up into shorter periods, 1926–9, 1934–7, 1946–50 (excluding 1948, no data being available in that year) and 1952–7 (excluding 1954, no data being available in that year). The results for the age groups 4–7 (or 3–6 after 1952) in the four periods are given in Figure 1B; two are significantly different from the bisector, although the differences are small.

Figures 2A and B give the same sort of information in a comparison between the East Anglian fishery and the Belgian spent herring fishery. From Figure 2A, it would appear that $Z_y \simeq Z_x$; in fact the East Anglian mortality is slightly higher, but not very much so. When we compare the three periods 1934–7, 1946–50 and 1952–8 in Figure 2B, it will be seen that the relationships are effectively bisector ones in 1934–7 and in 1952–8, but not in 1946–50, when $Z_y \neq Z_x$. This would imply that there were differences in apparent mortality between the fisheries at a time when the true mortality was not very high (see Appendix 1 of Part II for the mortality rates observed in the East Anglian fishery). It is possible that the Belgian spent fishery suffered an availability change during the period 1946–50, for at that time there was a changeover from bull trawls to pelagic trawls, which suggests a change in vulnerability.

Thus it is shown that there were no great differences in mortality between the component fisheries in the Southern Bight from 1930–58. This period is one during which a big change in mortality (from about 0·30 to about 0·80) was observed simultaneously in all the component fisheries. Variance about the regressions given in Figures 1 and 2 is due to sampling, mortality and year-classes. The total variance is low and so it is likely for that reason alone that the year-classes feeding the two fisheries contributing to the regression are common to them. To test this it might be possible to use the recruiting year-classes only, in the type of regression as given above; because there has been partial recruitment up to five years of age in the East Anglian fishery, it would be desirable to use the age groups three and four (or four and five) to represent the recruit year-classes.

This form of regression, which would be intended to estimate the likeness of year-classes in two fisheries, has two components of variance due to mortality. The first is the degree of mortality between the three-year and four-year-old fish (or four- and five-year-old fish); secondly, if total mortality is high, the percentages of three- or four-year-old fish are enhanced as compared with those when total mortality is low. Consequently, a regression might be generated merely by a change in total mortality during the period. Figure 3 shows firstly (3A) the percentages of fours and fives, marked separately, for the period 1926–37 in the East Anglian fishery and the Boulogne fishery; secondly (3B), the percentages of threes and fours, marked separately, in the same two fisheries for the period 1952–7; thirdly (3C), the percentages of fours and fives, marked separately, for 1930–7, in the East Anglian fishery and the Belgian spent fishery; fourthly (3D), the percentages of threes and fours, marked separately, in the same two fisheries for the period 1952–8. Regression lines are fitted to each age

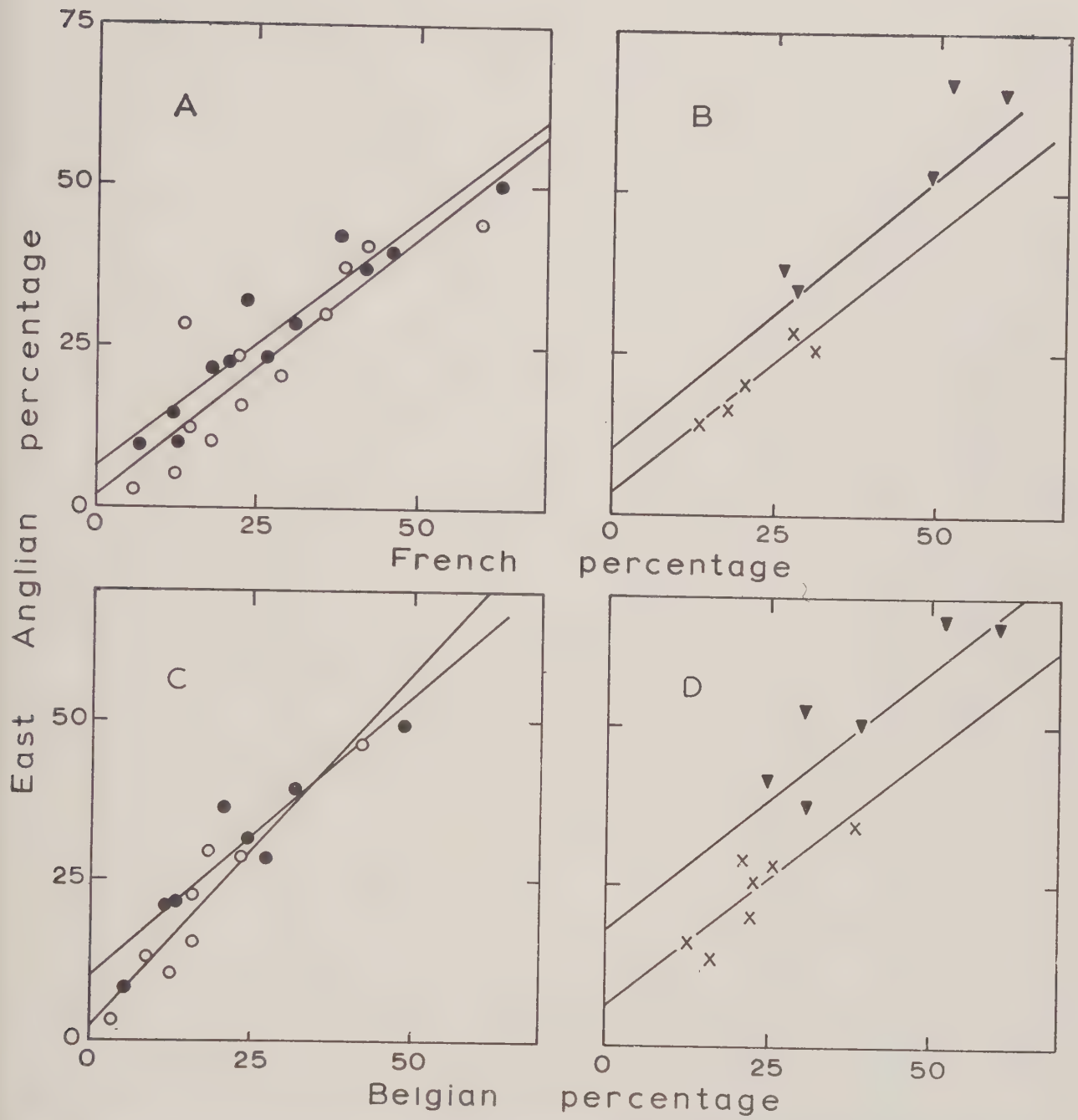

Fig. 3. A. *The regressions of percentage four-year-olds (●) and percentage five-year-olds (○) at East Anglia on the same at Boulogne for the period 1926–37; both regressions are significantly different from zero.*

B. *The regressions of percentage three-year-olds (▼) and percentage four-year-olds (×) at East Anglia on the same at Boulogne for the period 1952–7; both regressions are significantly different from zero.*

C. *The regressions of percentage four-year-olds (●) and percentage five-year-olds (○) at East Anglia on the same in the Belgian spent fishery for the period 1930–7; both regressions are significantly different from zero.*

D. *The regressions of percentage three-year-olds (▼) and percentage four-year-olds (×) at East Anglia on the same in the Belgian spent fishery for the period 1952–8; both regressions are significantly different from zero.*

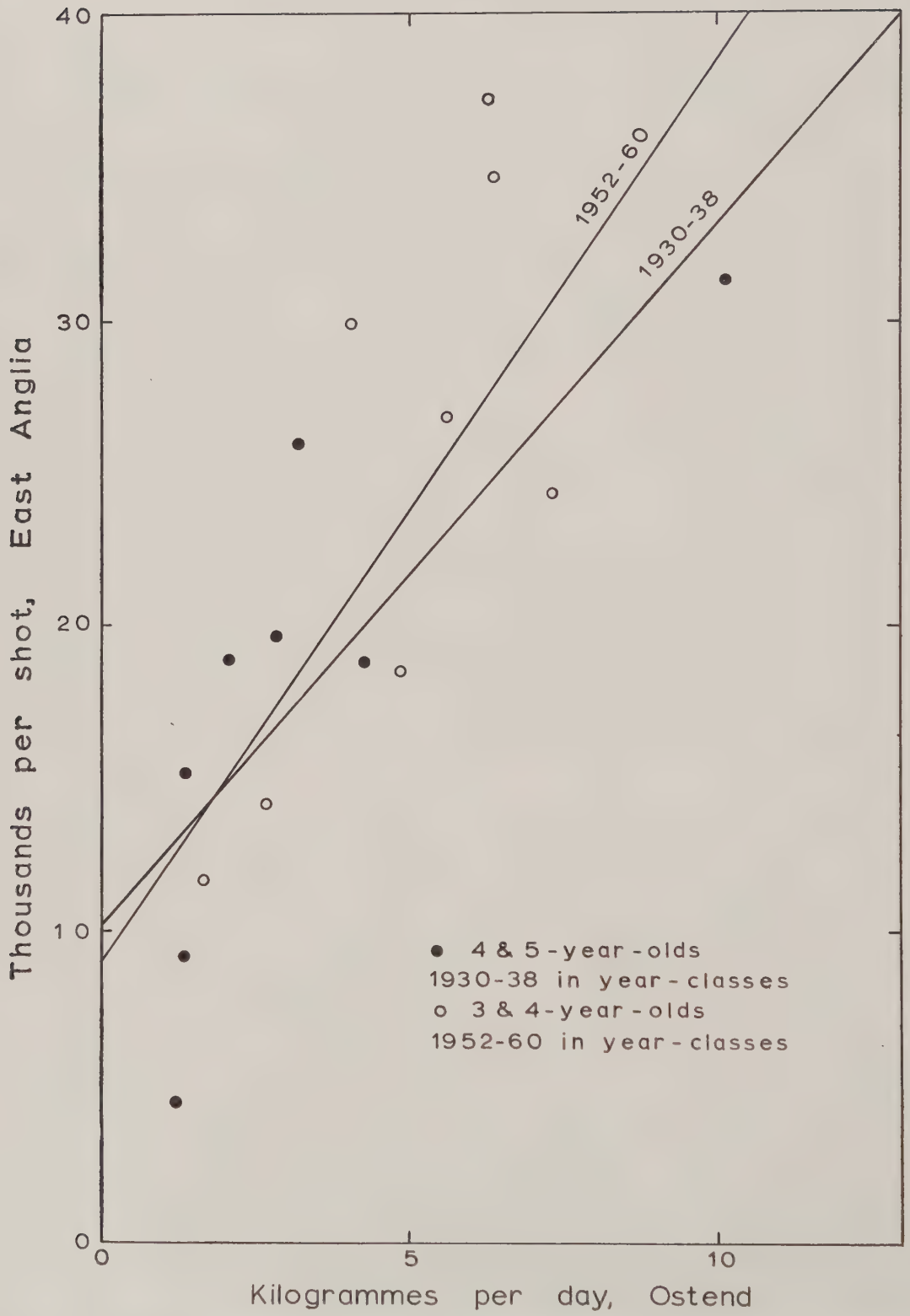

Fig. 4. *Regression of recruits in stock density at East Anglia on the same at Ostend. Both regressions are significantly different from zero.*

separately. Total mortality was common to all three fisheries throughout all the period; total mortality in the East Anglian fishery was steady (without upward or downward trend, see Appendix 1 of Part II) within each of the two periods used, but different in each period. Therefore the mortalities were the same in all three fisheries in each of the two periods. So the regression cannot be generated by a change in total mortality during either period. Regressions are fitted to the data for each age separately for each limited period; so the element of mortality in the differences between 4's and 5's or 3's and 4's has been eliminated. Therefore the regressions shown in Figure 3 demonstrate the likeness of year-classes. Each of the eight regressions is significantly different from zero; therefore we may conclude that the three fisheries in the Southern Bight are fed by common year-classes.

This problem may be attacked more directly. Figure 4 shows the relationship between year-classes in the East Anglian fishery and those in the Belgian spent fishery. The East Anglian observations are the numbers per shot of four- and five-year-old fish by year-classes from 1930–8 and the numbers of three- and four-year-old fish by year-classes from 1952–60 – the same periods as used in Figure 3. The Belgian observations are of the same ages in the same periods (Gilis, 1961b); in the first period results are from the bull trawl fishery and in the second period they are from the pelagic trawl fishery. The data for the period 1946–51 have not been used because at this time the fishermen changed from the bull trawl to the pelagic trawl, as noted above. A clear relationship (the regression is significantly different from zero; $p \leqslant 0{\cdot}02$, pre-war, $p \leqslant 0{\cdot}05$, post-war) is shown, meaning that the East Anglian fishery and Ostend fisheries exploit common year-classes. This point confirms the conclusion drawn from the comparison of percentage age distributions in Figure 3. Because there was correlation in year-classes between East Anglia and Boulogne and also between East Anglia and Ostend, there should be correlation in stock density between Ostend and Boulogne.

The comparisons between East Anglia and Boulogne (Figures 1A and B) and between East Anglia and Ostend (Figures 2A and B) show the condition of a stock common to the fisheries. In contrast, the comparison between Dogger and East Anglia shows the condition of distinct stocks. Figure 5A gives the relationship, in logs, between percentages of each age found on the Dogger (y) and percentages found in East Anglia (x); Figure 5B gives the same type of relationship for the periods 1923–9, 1934–6, 1946–50 and 1953–8. The slope of the regression is Z_y/Z_x and so, knowing Z_x (East Anglian mortality) from Appendix 1 of Part II (using that for the ages 5–7 as the best estimate), Z_y may be estimated, as in the following table:

	Z_y/Z_x	Z_x	Z_y
All ages 1923–58	0·65	0·48	0·31
1923–9	0·85*	—	—
1934–6	0·32	—	—**
1946–50	0·35	0·37	0·13***
1953–8	0·55	0·95	0·52

It is clear that a marked difference in total mortality has been found between the Dogger and East Anglia for the whole period. In the first sub-period 1923–9 no difference was found between the two groups; the second sub-period is a little short to be representative, but there is little doubt about the difference in the post-war period. This difference is in marked contrast to the apparent homogeneity within the Southern Bight fisheries, in which total mortality differences are small (see Table 5). The ratio Z_y/Z_x became $<1{\cdot}0$ between 1929 and 1934; an increase in recruitment did not take place on the Dogger at any time, despite the observed increase in recruitment to the Buchan pre-spawning

* Not significantly different from 1·0.

** There are only two observations of Z_x, one positive and one negative, and so no mean has been estimated.

*** This value is less than that estimated for natural mortality used later in the paper (page 75); it will be shown in Part II that Z_x was possibly underestimated during this period in the East Anglian fishery.

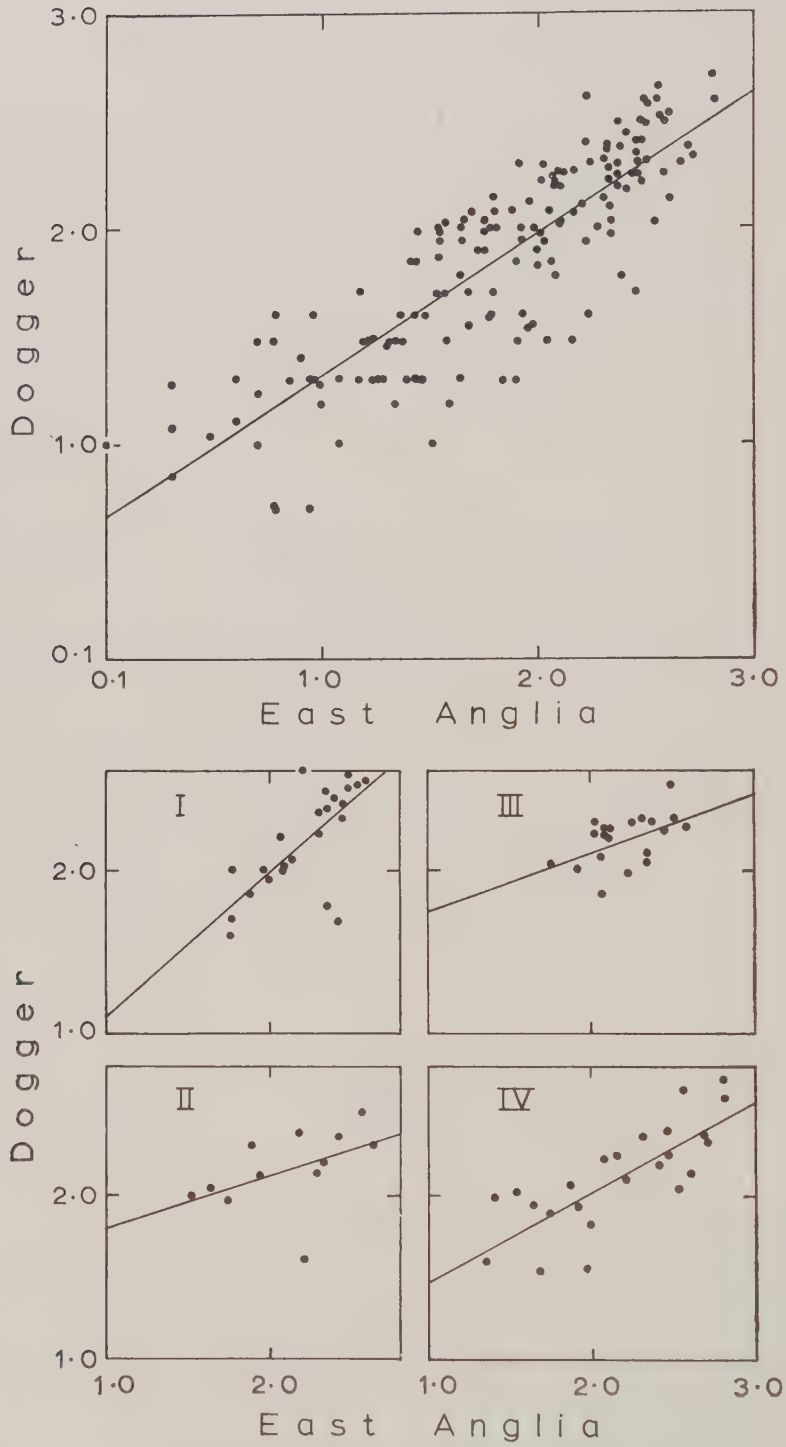

Fig. 5. A. *The relationship between the percentages of each age (in logarithms) on the Dogger on the corresponding percentage (in logarithms) at East Anglia from* 1923–58, *for all ages; the regression is significantly different from the bisector.*
B. *The relationship between the percentages of each age (in logarithms) (for the younger age groups) on the Dogger on the corresponding percentage (in logarithms) at East Anglia for four periods: I,* 1923–9, *ages* 4–7; *II,* 1934–6, *ages* 4–7; *III,* 1946–50, *ages* 4–7; *IV,* 1953–8, *ages* 3–6; *the regressions are all significantly different from the bisector, save the first.*

stock (Parrish and Craig, 1964). Such estimates of Dogger mortality should be compared with direct estimates – but these ones depend on the absolute value of the East Anglian mortalities, which are probably biased (see Part II).

The percentage age distribution method cannot be used further than to show a difference in coefficient of variation between the Dogger/East Anglian regression and the East Anglia/Boulogne regression. But the catch per effort technique can be used. Although such estimates have the added variance due to availability, they have less bias due to year-class variation than the percentage age distribution material. We look forward here to Figure 11 which shows the correlations between East Anglia and the Dogger spawning fishery, East Anglia and the Buchan spawning fishery, and between the Buchan spawning and the Dogger spawning fishery, all observations being in catch per unit effort of recruits. No regression has a slope significantly different from zero. This is in marked contrast to Figure 4 which shows a clear regression using catches per unit effort within the Southern Bight. Hence we may conclude that year-classes are common to the three Southern Bight fisheries and that there is no relation between them and those feeding the Dogger spawning fishery and the Buchan spawning fisheries.

The statistical data for the whole exercise are summarized in Table 1. It is concluded that the fisheries in the Southern Bight exploit a stock or stocks in which the mortality changes are common to them during periods of greatly changing mortality. It is also concluded that there is a community of year-classes formed in the Southern Bight which does not include any other spawning fishery (or pre-spawning aggregations such as the Fladen). The three fisheries in the Southern Bight exploit a spawning complex; fish in the East Anglian fishery are in maturity Stage V and are moving south to spawn, fish in the Channel fisheries are spawning, and fish in the Belgian fishery are spent. If the stock has any continuity from year to year, it will be complete at spawning and not separated into shoals feeding all over the North Sea. Therefore the fact that the year-classes are common to the three fisheries (through a period of pronounced recruitment change) and the fact that mortality is common to the three fisheries (despite sharp changes in mortality), means that the three fisheries in the Southern Bight must exploit a single stock.

If there is a single stock exploited by the Southern Bight fisheries, then the Dogger spawning stock is distinct from the Southern Bight stock. Evidence of distinctness can be found in the study of vertebral sums (Buchanan Wollaston, 1933); the difference in *VS* between Dogger and Downs stocks is maintained through all age groups (Zijlstra, 1958). If the meristic difference is real, mixing, if present, is low and constant and does not increase with age. The differences in l_1 distributions (Burd and Cushing, 1962) between Dogger and Downs, the mean for the Dogger being larger than that for the Downs, combined with the consistency of l_1 distributions within a year-class in the East Anglian fishery, lead to the same conclusion – that mixing between the two stocks is low and does not increase with age. It seems therefore that the herring, once they appear as a recruiting year-class, return to the Southern Bight year after year from the northern North Sea and, as a spawning stock, do not emigrate or suffer immigration to any noticeable extent. This sentence defines the limited meaning of the phrase 'Downs stock'.

Zijlstra (1958) goes further than this and believes that herring return year after year to their native spawning grounds in some topographical detail – because of the constancy of difference in VS between spawning grounds, particularly Ailly and Sandettié. It is possible that fish from different spawning grounds become mixed at recruitment and that the recruited fish remain in the stock until the year-class is extinguished; it is equally possible that fish from different spawning grounds become segregated even in the recruitment mechanism. The work of Baxter (1959) on fecundity has shown that there is a clear difference in egg number and egg size between Buchan spawners and East Anglian fish. Again, Muzinic and Parrish (1960) have found that there is a difference in the head length/total length ratio between Buchan spawners and East Anglian fish, which increases with age. As both

Table 1. *Statistical summary of the regressions shown in Figures* 1, 2 *and* 5

	Southern Bight				Dogger/East Anglia	
	East Anglia/French		East Anglia/Belgian		Z_y/Z_x	
	Slope and its standard error		Slope and its standard error			
All ages (mortality)		0·97 ± 0·027		1·17 ± 0·045		0·65
Ages 4/5 or 3/4 (year-classes)		0·91 ± 0·071		0·96 ± 0·078		
Ages 4–7 or 3–6	1926–9	0·98 ± 0·115			1926–9	0·85
	1934–7	0·74 ± 0·088	1934–7	1·06 ± 0·082	1934–7	0·32
	1946–50	0·98 ± 0·148	1946–50	1·33 ± 0·237	1946–50	0·35
	1952–7, excl. 1954	1·21 ± 0·059	1952–8	1·23 ± 0·081	1953–8	0·55

Dogger/East Anglia

$$(ln\ _{\text{Dogger}} - 0{\cdot}67) = 0{\cdot}65\ ln\ _{\text{East Anglia}}$$

$$\bar{y}_{(1923-30)} = 1{\cdot}674$$

$$\bar{y}_{(1953-58)} = 1{\cdot}658$$

papers deal with average values of a measured character, these results may be classed as studies of meristic characters. They are more precise differences than those found in vertebrae or in keeled scales, because sharper differences were found on rather small samples.

From a management point of view, Zijlstra's concept is the same as that given above, which states that the stock in the Southern Bight is distinct and remains so during its exploited existence. But Zijlstra's view is of some importance from the wider biological point of view. The spawning grounds in the Southern Bight are of very limited extent (Sandettié, Cap Gris Nez, Ailly or Creux St Nicolas) each of which is only about a mile or so across; spawning probably takes place on these restricted grounds at a reasonably constant time – to within a week or fortnight. The biological problem here is not only one of stock segregation but one of either homing, or of precise navigation, to a particular small spawning ground.

3. THE BIOLOGY OF THE NORTHERN NORTH SEA HERRING

We may now turn to the biology of the autumn-spawning herring in the northern and central North Sea. There are two groups native to the northern and central North Sea, the Buchan and Dogger autumn spawners; the latter have been loosely designated as the Bank stock.* The Downs stock or the Sandettié–Ailly spawners visit the northern and central North Sea in summer but they leave it in late summer to move south to their spawning grounds. The two groups native to the northern and central North Sea will be briefly characterized, the evidence for the basic migrations from tagging experiments will be summarized, and then the evidence for the presence of the Downs stock in the

* The 'Bank' stock as defined by Johansen (1924) and Le Gall (1935) included all herring spawning between Sandettié and the Buchan grounds. The separation of the German-termed 'Downs' stock is justified in Cushing and Burd (1957), in this paper, and in the Report of the North Sea Working Group on Herring (ICES, 1965). The Working Group Report also separates the Buchan spawners from the (Dogger) 'Bank' stock.

northern and central North Sea will be examined. Spring spawners live in the northern North Sea and must be separated from the autumn-spawning groups. So a brief biology of northern North Sea spring spawners will be given first.

SPRING SPAWNERS

Adult fish move from the spawning grounds off the Scottish coasts to the feeding grounds in the northern North Sea in early summer. They reach the Fladen ground in September and possibly remain there until January, as shown in pre-war and post-war data (Wood, on the 1931 year-class, 1937; Andersson, 1950). The proportion of spring spawners on the Fladen ground is small (5–10%; Schubert, 1957, and Saville, personal communication). Spring spawners are found in high proportions on the Viking Bank, Patch, Bressay Bank and Shetland at various seasons.

TAGGING RESULTS

Table 2 shows the combined results of the relevant tagging experiments that have been carried out on the North Sea autumn-spawning stocks of herring.

Table 2. *A summary of all the North Sea recaptures from tagging experiments on the North Sea autumn-spawning herring.*

Skagerrak liberations (Höglund, 1955)

	July	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*
Skagerrak	—	—	—	—	—	—	—	—			
Egersund Bank	—	5	2	—	—	—	—	—			
Fladen	1	8	4	—	—	—	—	—			
Gut	—	—	4	1	—	—	—	—			
Dogger	—	—	16	22	4	—	—	—			
Whitby	—	—	3	1	—	—	—	—			
W. Hole	—	—	—	—	1	—	—	—			
Winterton	—	—	—	—	—	—	—	—			
Sandettié	—	—	—	—	3	—	—	—			
Horns Reef	—	—	—	—	—	—	—	1			
Hantsholm	—	—	—	1	—	—	—	—			

Dogger liberations (Höglund, 1955)

	Sept.	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*Mar.*	*Apr.*	*May*	*June*	*July*	*Aug.*
Dogger	2	4	—	—	—	—	—	—	—	—	—	—
Winterton	—	—	2	—	—	—	—	—	—	—	—	—
Sandettié	—	—	3	1	—	—	—	—	—	—	—	—
Skagerrak	—	—	—	—	1	6	1	—	1	—	—	—
Fladen	—	—	—	—	—	—	—	—	—	—	—	1

Shetland liberations

Patch	1
Scottish north-east coast	4
Fladen	121
Gut	3
Dogger	6
Skagerrak	7
Channel	1

Scottish north-east coast liberations

Shetland	1
Fladen	254
Gut and English north-east coast	14
Dogger	29
Skagerrak	7
East Anglia	6
North Minch	1

(Wood, Parrish and McPherson, 1955)
(Parrish et al., 1954, 1956, 1957)

The experiments carried out by Höglund in the Skagerrak (liberation in February) and on the Dogger (liberation in October) show quite clearly that the herring in the northern and central North Sea move in an anti-clockwise circuit, from the Skagerrak in February to the Fladen, Gut and Dogger

in that order in the following summer, and from the Dogger in September to the Skagerrak six months later and Fladen eleven months later. The direction of movement is that of the main North Sea swirl (Böhnecke, 1922; Tait, 1934). The herring may take their orientation from it, but it is likely that the timing of their migration is independent of the water movements.

It has been suggested above that there is a segregation of fish to the spawning grounds. Dogger or Buchan spawners were tagged in the Skagerrak, and 13 were recovered from the Fladen and 42 from the Dogger; three were recovered from Sandettié, two tagged in early 1951 and one early in 1952. It is possible that two of these (1951 tagging) were associated with the recruitment of fish in 1951 to East Anglia with a low VS and a high l_1 distribution (as if there had been a proportion of Bank fish amongst them), but this does not account for the tag recovered at Sandettié from the 1952 tagging. However, it can be said that few fish reached the Southern Bight as compared with Fladen and Dogger. In fact, $0{\cdot}13 \times 10^{-4}$ tags/ton of fish were recovered in the Southern Bight as compared with $3{\cdot}02 \times 10^{-4}$ tags/ton of fish (Cushing and Burd, 1957) caught on the Fladen, Gut and Dogger. Fish were recaptured after periods of up to 1 300 days at liberty and one tag was recovered at Sandettié nearly two years after tagging. So it is unlikely that the contrast between the proportion of tags recovered on Fladen, Gut and Dogger and that recovered in the Southern Bight was due to tagging mortality. Thirty times as many tags were recovered from the Fladen, Gut and Dogger as from the Southern Bight, and so only a very small proportion of the fish reaching the Skagerrak go to the Southern Bight.

When we consider the Shetland experiments, we find that only 1 tag out of 143 was recovered south of the Dogger. None tagged after June was recovered south of the Fladen. Most fish were tagged in May, June and July; 16 fish tagged in May and June were recovered from the Gut, Dogger and Skagerrak, between August and the following February, which covers the time period during which fish might be expected to appear in the Southern Bight. This is to be contrasted with the one tag recovered from the Southern Bight, and so it is reasonable to conclude that very few fish of the Downs stock return to the Southern Bight from Shetland. We may also conclude that the Dogger fish have moved south by the end of June or the beginning of July.

It is likely that the loss of tags in the Scottish experiments was higher than that in the Swedish experiments, because very few fish, if any, were returned after one year. The Skagerrak fishery takes place some five to six months after the East Anglian fishery and so we would expect more Scottish tags to have disappeared by the time the Skagerrak fishery took place. From fish tagged on the Scottish north-east coast, 6 were recovered from East Anglia and 7 from the Skagerrak. We may consider the loss of tags to be roughly equal in East Anglia and the Skagerrak, or a little more in the later fishery. To counter this, it is probable that the gears used in the Skagerrak fishery are more effective in collecting tagged fish than are the drift nets at East Anglia (see Höglund, 1955). A reasonable conclusion would be that Bank and Downs fish were mixed off the Scottish north-east coast. It was noted above that most of the fish which were recovered on the Dogger were tagged before mid-July in the Buchan pre-spawning fishery, and that many of these fish were Dogger recruits.

The conclusions from these experiments are that a very small proportion of Skagerrak fish reach Sandettié, that very few Shetland fish go south of the Dogger, that Dogger fish leave the Scottish north-east coast before July, and that some East Anglian fish have spent the previous summer on the Scottish north-east coast.

THE BUCHAN AUTUMN SPAWNERS

The Buchan pre-spawning fishery takes place off the north-east coast of Scotland from April to July. It is composed mainly of virgin recruiting fish, some of which probably join the Buchan spawning

fishery in late July and August (Wood, on the 1928 year-class; 1937). One component of the Buchan pre-spawning fishery during the fifties was a proportion of Dogger virgin spawners. This was shown by tagging, for many of the Dogger recaptures had been liberated on the Scottish north-east coast. A further most interesting point is that most were liberated before July (Wood, Parrish and McPherson, 1955; Parrish et al., 1954, 1956, 1957).

Fish liberated on the Scottish north-east coast after July reach the Fladen ground or remain on the Scottish north-east coast (Wood, Parrish and McPherson, 1955). The age distributions of autumn spawners from the Patch and Shetland and the Buchan spawning fishery show some resemblances, particularly with respect to the 1928 year-class (Wood, 1937). Similarly, the age distributions of autumn spawners from Shetland, Viking and Utsire in recent years tend to resemble each other (Schubert, 1957, 1958, 1959 and 1960). The clearest correlation between age distributions is that shown by Andersson (1950), who compared the autumn Fladen age distributions with those of the Skagerrak in the following winter. Common to both, during the war and just after it, were the strong 1940 and 1942 year-classes. These year-classes can be seen in age distributions from the Buchan spawning fishery, Shetland (Parrish and Craig, 1964) and the Fladen (Gilis, 1957, Schubert, 1957) up till 1953 or 1954. The Scottish material in 1951–3 shows that in general these very old fish enter the Fladen fishery in September (Wood et al., 1952, Parrish et al., 1953); German material in 1953 and 1954 shows them on the Fladen ground in August as well as September (Schubert, 1957). The fish on Fladen in September were mainly spent and it is likely that these very old fish were Buchan autumn spawners. Hence the circuit of Buchan spawners during the year resembles that of Dogger spawners. The spent fish appear on Fladen in September, in the Skagerrak in February, and on the Viking Bank in spring; at Shetland in summer are found the ripening fish before they spawn off the Scottish coast. An interesting point is that if some fish can survive to the age of fourteen or fifteen years in the Buchan spawning fishery, the natural mortality rate must be quite low. The Buchan autumn spawners appear to move round the North Sea in a circuit: from the Turbot Bank (and other local spawning grounds) to Fladen, Skagerrak, Utsire, Shetland, Patch in that order, and back to the Turbot Bank.

THE DOGGER AUTUMN SPAWNERS

From the results of the Scottish tagging experiments (Wood, Parrish and McPherson, 1955) maturing virgin fish appear to be present in the Buchan pre-spawning fishery in May and leave by mid-July, moving south to spawn on the Dogger by September and October. From Höglund's (1955) tagging experiment on the Dogger, the fish move into the Skagerrak after spawning. From there they probably move out towards the Egersund Bank, and then in the following April are exploited by the Aberdeen 'boxing' fishery. By May or June of that year, they reach the Scottish north-east coast and the Fladen. From these grounds the fish migrate south in midsummer to the Dogger for the second time, where they spawn (Figure 6).

THE DOWNS SPAWNERS

After spawning, tagged fish of the Downs stock have been recovered from the Silver Pit (Bolster, 1955) and one either from the Fladen ground or the Farne Deep (Ancellin and Nédelèc, 1959). Burd (in Burd and Cushing, 1962) has shown that the Downs fish move north into the Shields fishery from the spawning ground in early summer, and also that they move south into the Shields fishery in July and August. Krefft (1954) has suggested that they are found in the area of the Gut and Long Forties

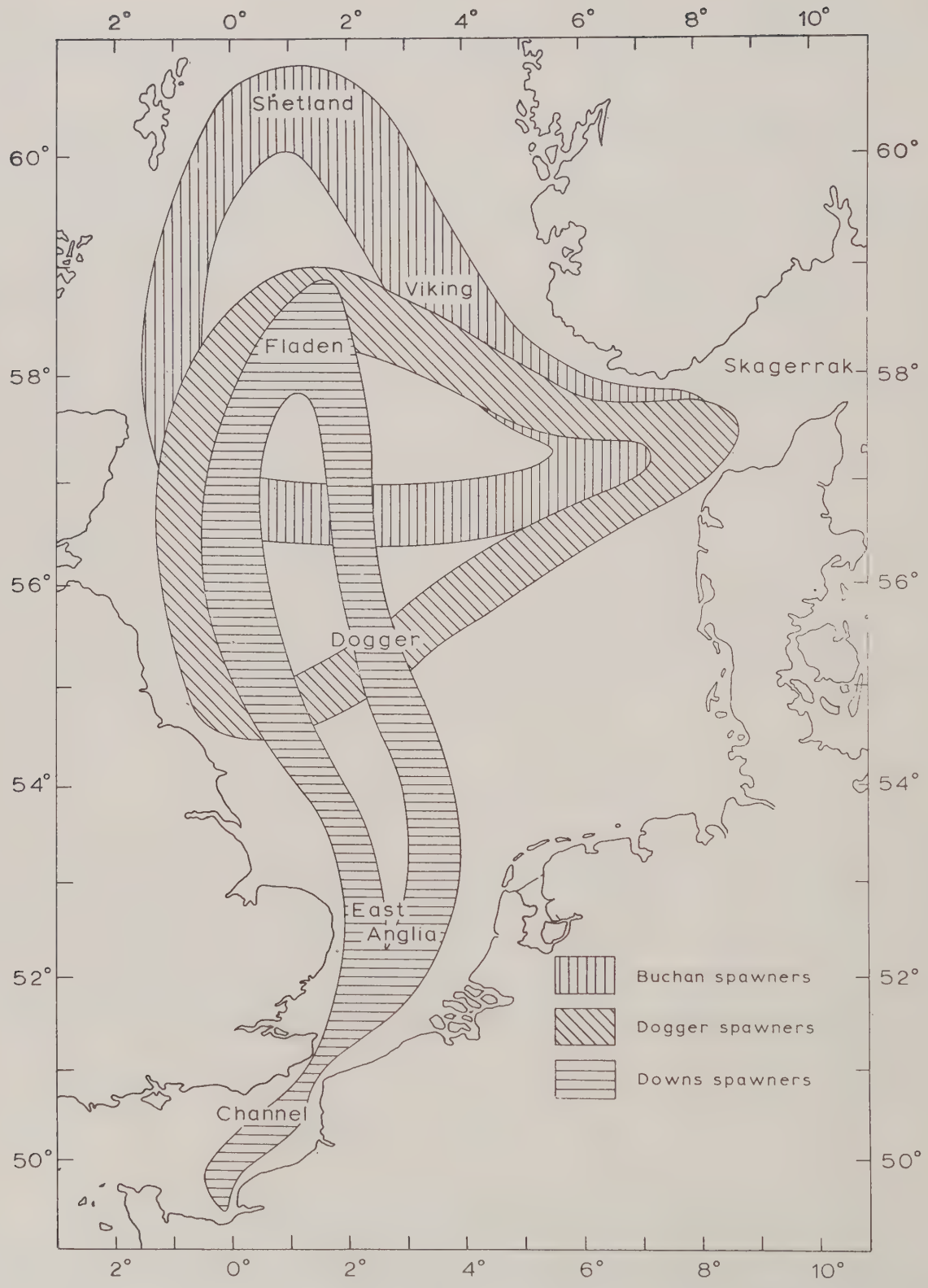

Fig. 6. *Hypothetical migratory circuits of the adults of the three spawning groups, Buchan, Dogger and Downs.*

in the summer time (Krefft's Figure 4). There is no evidence from tagging, from age distributions or from meristic characters that fish of the Downs stock reach the Viking Bank, the Patch or the Utsire Bank.

It is concluded that there is sufficient evidence to show that fish of the Downs stock are to be found in the extensive feeding areas in the western North Sea between Flamborough and the Patch, possibly excluding the Patch itself. Wood has written (1937) 'Late autumn or southern North Sea autumn spawners are found in May and June in Shetland waters, but the greatest concentrations are off the north-east coast of Scotland, where in May, June and July, they are associated with shoals of young north-western North Sea autumn spawners, which are immature or maturing for the first time. Like the spring spawners, they withdraw from the drift net grounds in July, and many of them, particularly the older fish with four or more winter rings on their scales, are found on the Fladen ground and give a start to the herring trawl fishery in late July. By the middle of September, the majority of them have left these grounds in a movement southwards towards their spawning grounds in the middle or southern North Sea and the eastern entrance to the English Channel.' This classically clear statement is based on evidence of VS, K_2 and age distributions of the Buchan pre-spawning, Buchan spawning, Fladen and East Anglian fisheries from 1932–5; in particular, it was shown that prominent year-classes appearing in the Buchan pre-spawning fishery and at Fladen, but not in the Buchan spawning fishery, were also prominent in East Anglia.

THE FLADEN GROUND

The central puzzle in the separation of Downs spawners from others in the northern North Sea is the composition of the stocks on the Fladen ground. Wood (1937) has shown that Buchan spawners, Dogger spawners and spring spawners are found there and has suggested that 'Lincolnshire coast' spawners (of high vertebral sum and high keel-scale count) were found there. One of his reasons for believing this is the following table from his 1930 paper (Table 3). The separation of spawners and ripening fish on the Scottish north-east coast is quite clear. Taking the fish of five years of age, which we may assume to be fully recruited, we see that there is a consistent difference of approximately 2 cm in length for age between the spawners and the ripening fish. This is the present order of difference between East Anglian and Buchan spawning fish. The difference is less marked amongst the three-year-olds and the oldest fish. But there is a remarkable difference in age distribution patterns of maturing fish and of spawners. On the Fladen ground, using the observations of length for age and comparing them with those off the Scottish north-east coast, it is clear that all maturity stages were to be found there. This is also the conclusion from the observations made by Scottish and German workers during the fifties (Wood et al., 1952, Parrish et al., 1953, 1954, 1956, 1957, 1958, 1959, Schubert, 1957, 1958, 1959, 1960).

CONCLUSION

From this brief and limited discussion on the biology of the herring in the northern and central North Sea the following tentative conclusions may be drawn:

(*a*) Spring spawners are found on the Fladen between mid-September and January; they are also found on the Viking Bank, Bressay Bank and Shetland. From the end of May to August on the Scottish north-east coast, Fladen, Gut and Dogger the proportion of spring spawners is low.

(*b*) Recruits to the Buchan autumn spawners are found in the Buchan pre-spawning fishery from May to July; spawning takes place on the Turbot Bank and off Orkney in August and September. In these months spent fish are found on the Fladen but predominantly in September. It is likely that fish of the same stock are caught on the Viking Bank in February and March, and in Shetland in summer.

Table 3. *Samples from the Scottish north-east coast and the Fladen ground* – 1924
(from Wood, 1930)

	Maturities %						Age composition %							Mean size of age groups (cm)						
	I–II	III	IV	V	VI	VII	3	4	5	6	7	8	9+	3	4	5	6	7	8	9+
									Scottish east coast drift-net grounds											
									Spents predominant											
Aug. 12	5·0	21·1	16·8	7·4	4·7	44·9	7·1	17·6	45·5	17·0	8·8	1·9	1·9	23·6	24·3	26·3	25·7	28·7	29·1	30·1
Aug. 20	1·5	8·4	7·7	3·3	1·5	77·7	4·4	9·4	59·5	13·1	8·7	1·8	2·9	23·0	24·6	26·4	26·3	28·2	29·8	30·4
Sept. 5	3·3	14·6	13·2	2·4	5·7	60·8	4·2	17·8	35·0	21·1	16·0	2·7	3·0	23·2	23·8	25·5	25·4	28·2	28·2	29·4
									Spawners predominant											
Aug. 6	—	—	1·4	19·7	78·0	0·9	1·9	4·2	77·3	4·7	6·5	3·7	1·4	24·7	25·3	26·7	27·7	28·7	29·4	30·0
Aug. 20	—	—	5·5	16·6	56·1	21·9	5·4	12·2	73·1	4·0	5·4	—	—	22·5	25·8	26·2	26·7	28·0	—	—
Sept. 1*	—	—	—	5·4	94·2	0·4	—	1·9	28·0	16·8	40·3	—	—	—	25·2	26·6	27·5	28·5	29·4	30·4
Sept. 12	—	2·4	17·6	38·2	39·4	2·4	89·2	6·2	2·7	1·1	0·8	—	—	22·8	23·4	26·2	26·0	27·3	—	—
									Maturing											
Aug. 20	21·3	39·4	19·8	5·2	2·1	12·1	3·9	35·2	34·2	24·8	0·9	0·4	0·4	23·0	23·8	24·4	24·6	26·0	29·0	30·0
Aug. 21	5·3	30·1	28·8	25·1	8·5	2·1	1·6	27·0	29·4	24·6	13·2	1·6	2·8	23·0	23·8	24·6	25·2	28·1	28·7	29·5
Aug. 27	1·0	15·9	46·0	32·6	4·6	—	14·8	37·3	28·0	15·5	3·1	—	1·2	22·9	23·8	25·3	26·3	27·1	—	29·2
Aug. 27	3·4	43·2	43·0	9·6	0·4	0·4	33·0	57·9	6·9	1·5	0·6	—	—	23·1	23·4	24·9	24·1	27·6	—	—
									Fladen trawling ground											
Aug. 6*	—	—	—	—	—	—	—	—	—	—	—	—	—	—	23·5	24·5	25·7	27·1	27·2	29·0
Aug. 19	9·1	36·3	34·0	10·2	6·5	3·8	—	5·4	20·7	38·5	27·0	5·1	3·2	—	24·5	25·5	25·6	26·4	27·6	29·1
Sept. 3	4·3	23·8	30·7	20·6	8·4	2·2	—	0·3	12·2	43·1	30·1	6·1	8·0	—	26·0	25·5	26·1	26·8	27·3	29·6
Sept. 10	2·7	43·3	31·0	11·4	1·4	9·3	—	6·0	29·6	50·0	9·5	2·2	2·5	—	23·9	24·9	25·4	26·0	27·9	29·6
Aug. 26–Sept.	—	—	—	—	—	—	—	—	—	—	—	—	—	22·0	23·9	24·7	25·5	26·7	28·5	29·5–30·0
Sept. 16*	—	—	—	—		—	—		—	—	—		—	—	25·0	25·6	26·5	27·6	28·3	29·0–31·0

* Samples were caught by drift net except those marked with an asterisk, which were trawl-caught.

(*c*) Recruits to the Dogger spawning fishery are probably found in the early part of the Buchan pre-spawning fishery, having moved south to spawn by July. The older fish probably leave the Fladen at about the same time. After spawning the fish move into the Skagerrak and on to the Egersund Bank; subsequently they are exploited by the Aberdeen 'boxing' fishery and possibly by the early Fladen fishery.

(*d*) The Downs fish move north through Shields and have been identified by meristic characters in the Gut and on the southern edge of the Fladen in summer. It is likely that they leave the Buchan pre-spawning fishery and move on to the Fladen ground in July, before moving south by September. The Downs recruits move through the Shields fishery in July, but it is likely that the older fish come later.

(*e*) There are fish in all maturity stages up to and including stage V on the Fladen in July and August. From the type of evidence presented by Wood (1930) the spawning fish are distinct from the maturing fish. Because the difference of 2 cm in length for age is of the order of the present difference in length for age between Buchan and Downs spawners, it is possible that Downs spawners are to be found on the Fladen. Possible migratory routes of the three spawning groups are given in Figure 6.

4. RECRUITMENT TO THE NORTH SEA STOCKS

Much argument in the subsequent sections depends on whether the level of recruitment to the Buchan (spawning), Fladen, Dogger, Dogger (spawning) or Southern Bight (spawning) fisheries changed during the period 1930–58; here we differentiate between the three spawning fisheries and the two other fisheries on the Fladen and around the Dogger.* Cushing and Burd (1957) showed that the pattern of recruitment to the East Anglian fishery from 1924–55 changed in the years 1950–2, and that this was only part of a slower and more gradual change that had been taking place since the twenties. From 1924–8 recruitment took place at three, four and five years of age, the majority entering the fishery at five. From 1929–50, half of the recruits came in at three and half at four years of age. From 1952 onwards, the majority of fish recruited at three. Figure 7 shows the recruitment as at three years of age to the East Anglian fishery from 1926–58, uncorrected for the efficiency change referred to in Parts II and III. Between 1946 and 1961 it is likely that the apparent stock density of the Downs stock has been biased upwards due to an increasing efficiency of the drifter shot. Thus true stock density and hence recruitment has declined. The data in this section are not corrected for this increase in efficiency. This is because the effects of changes in abundance or in apparent abundance are minimized in the method to be described in Section 5.

From 1924–34, the East Anglian data are reported in crans with no estimates of numbers per cran. From length per age, weight per age and hence average weight, a factor was calculated for converting weight to numbers during those years. In a mimeographed paper to ICES (Cushing 1958 b), this factor was omitted; a figure corresponding to Figure 7 was reproduced by Parrish (1962). It shows an apparent increase in the recruitment (due to the omission of this factor) which does not in fact exist. So the data given in Figure 7 are composed of two types: (*a*) crans/landing raised by a factor raising crans to numbers from 1924–34, (*b*) numbers/shot from 1935–8 and from 1946–58.

Estimates of total mortality between the ages of five and seven, Z_{5-7} (from Appendix Table I of Part II), and an estimated natural mortality, M, of 0·2, were used to calculate the recruitment. Some independent estimates of natural mortality will be presented below.

* The spawning fishery on the Dogger will be named the Dogger spawning fishery. The fishery for all maturity stages in and around the same area, which might be a mixture of the Downs and Dogger spawning stocks, will be named the Dogger fishery.

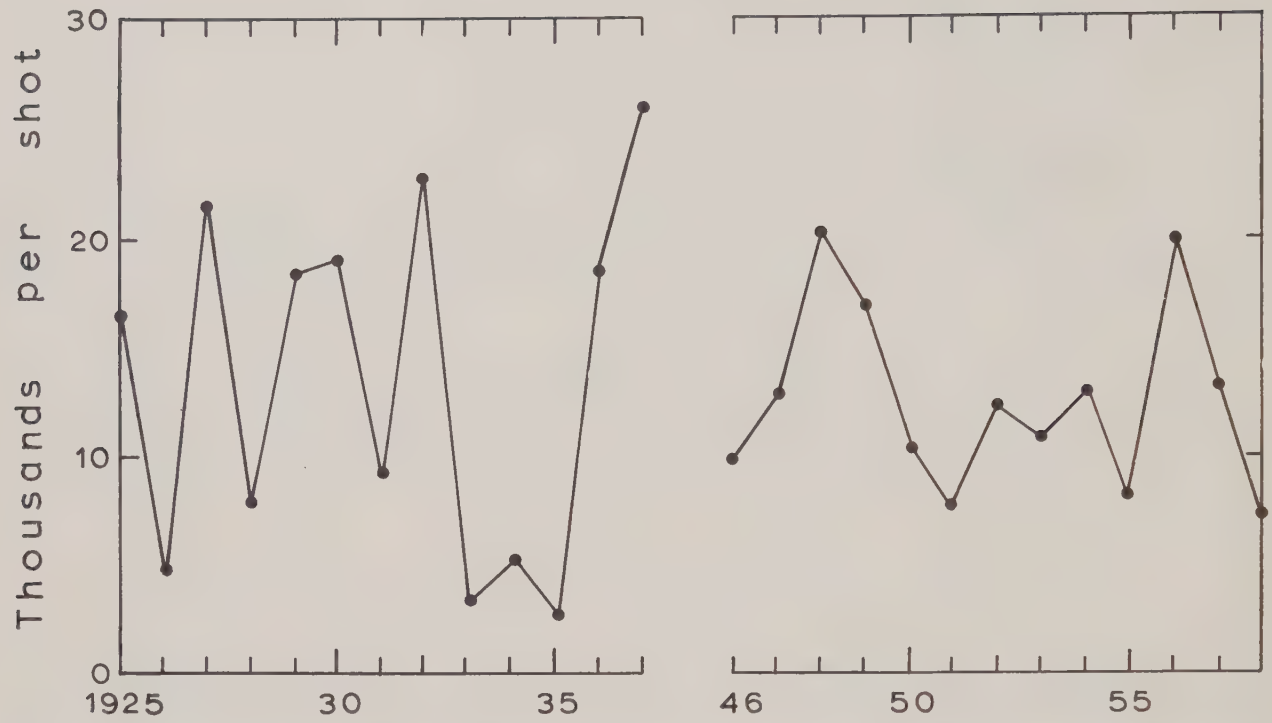

Fig. 7. *Total recruitment to the East Anglian fishery, in thousands per shot as at three years of age, from* 1925–58*; these estimates are uncorrected for the efficiency change referred to in Part II and Part III.*

Let $R_3 = r_3 + r_{3\cdot1} + r_{3\cdot2}$

$= n_3 + (n_4 - r_3e^{-Zt})\, e^{Mt} + (n_5 - n_4e^{-Zt})\, e^{2Mt}$

where R_3 is the stock density of recruits of a year-class as at three years of age;

where n_3, n_4 and n_5 are the stock densities of fish at three, four and five years old respectively;

where r_3, r_4 and r_5 are the stock densities of recruits at each age group, three, four and five, and r_3, $r_{3\cdot1}$, $r_{3\cdot2}$, the same stock densities as at three years of age;

where M is the instantaneous natural mortality rate;

where Z is the instantaneous total mortality rate;

where t is one year.

Figure 7 shows that recruitment to the East Anglian fishery, in uncorrected stock density as at three years of age, has apparently been steady from 1925–58, with no upward or downward trend; the range of variation is of the order of ten times and the coefficient of variation is $\times 2{\cdot}5$. If natural mortality were underestimated, each value of recruitment in Figure 7 would be increased and vice versa. Further, if either $(n_4 - r_3e^{-Zt})$ or $(n_5 - n_4e^{-Zt})$ is large, such an underestimate would increase. In view of the changes of recruitment pattern that have taken place since 1924, this sort of underestimate might have been greatest in 1924–8 and least in 1952–8. Thus as there is no trend in Figure 7, an underestimate of natural mortality might generate a slight downward trend from 1925 to 1938. Had there been a trend in true natural mortality, upward or downward (for which there is no evidence), a trend could appear in the values of recruitment. The values of natural mortality given later in this paper provide no such evidence of trends in recruitment.

It is likely that the Belgian age distributions from the Dogger in October represent mainly Dogger spawners (Gilis, 1957, 1958 a, b and c, 1959, 1961 a, 'région centrale de la Mer du Nord'). Table 4 gives the proportions of fish in maturity stages VI, VII and VII/II on the Dogger in October.

Table 4. *The proportion of fish (in %) in stages VI, VII and VII/II on the Dogger in October contributing to the Belgian age distributions from 'la région centrale de la Mer du Nord' (Gilis, 1957, 1958 a, b and c 1959, 1961 a)*

1949	89·8
1950	46·3
1951	28·6
1952	30·7
1953	51·3
1954	41·5
1955	64·0
1956	No sample
1957	76·9
1958	12·0
1959	59·1

The low values in 1951, 1952 and 1958 mean either that some East Anglian fish were present or that the ratio of spawned to unspawned fish in the fishery in October varies. The average value of the ten samples in Table 4 is 50% ; as a fair proportion of fish in stage V must also have been Dogger spawners, it is reasonable to assume that the majority of fish in stages VI, VII and VII/II were Dogger spawners.

In the early fifties, two extensive biological changes took place. The first was the change in the recruitment pattern in 1950–1, which was widely spread over the North Sea (Cushing and Burd, 1957; Parrish and Craig, 1957; Burd and Cushing, 1962). The second, which was probably a facet of the first, was the sharp increase in the magnitude of recruitment to the Buchan spawning fishery in 1953, increasing the total stock in that fishery substantially by 1955 (Parrish and Craig, 1964). The effect of the recruitment change on the Downs stock was to make recruitment complete at three years of age; on the Buchan and Dogger spawning stocks, its effect was to make recruitment nearly complete at four years of age, but not quite. In the Buchan and Dogger spawning fisheries a natural mortality rate of 0·2 was taken and values for Z for the years cited were estimated from catches/effort published by Parrish and Craig (1964) and Gilis (1957, 1958 a, b and c, 1959, 1961 a). Figure 8 shows the percentages of recruitment as at three, four and five years of age in the Buchan spawning fishery, the Dogger spawning fishery and the East Anglian fishery from 1949–57. It will be seen that from 1953–7, East Anglian recruitment was practically complete at three years of age, whereas in the Buchan spawning fishery and in the Dogger spawning fishery, a peak in the proportion of three-year-old recruitment was reached in 1952 or 1953, after which it declined. This apparent retrogression of the proportions of recruitment at the ages three, four and five to the Buchan and Dogger spawning stocks is of the greatest interest. However, we are more concerned here with the unexpected persistence of partial recruitment to the two northern stocks during the fifties.

Figure 9 shows the course in time of total recruitment as at three years of age to the Buchan spawning fishery from 1930 to 1958 and to the October Dogger fishery from 1949 to 1957. It will be seen that the recruitment to the Dogger spawning fishery has apparently declined from 1949 to 1957. However, examination of further data from Dutch sources (year-classes 1943–58) in the Herring Assessment Group Report (1964) shows that no downward trend is evident. The outstanding year-class in the Dogger spawning fishery was the 1946 class. Recruitment to the Buchan spawning fishery has risen by about three times since 1953.

The techniques used on the spawning stock fisheries cannot be readily applied to the Fladen and Dogger fisheries because the German data series from 1930 onwards is broken (Krefft, Schubert and

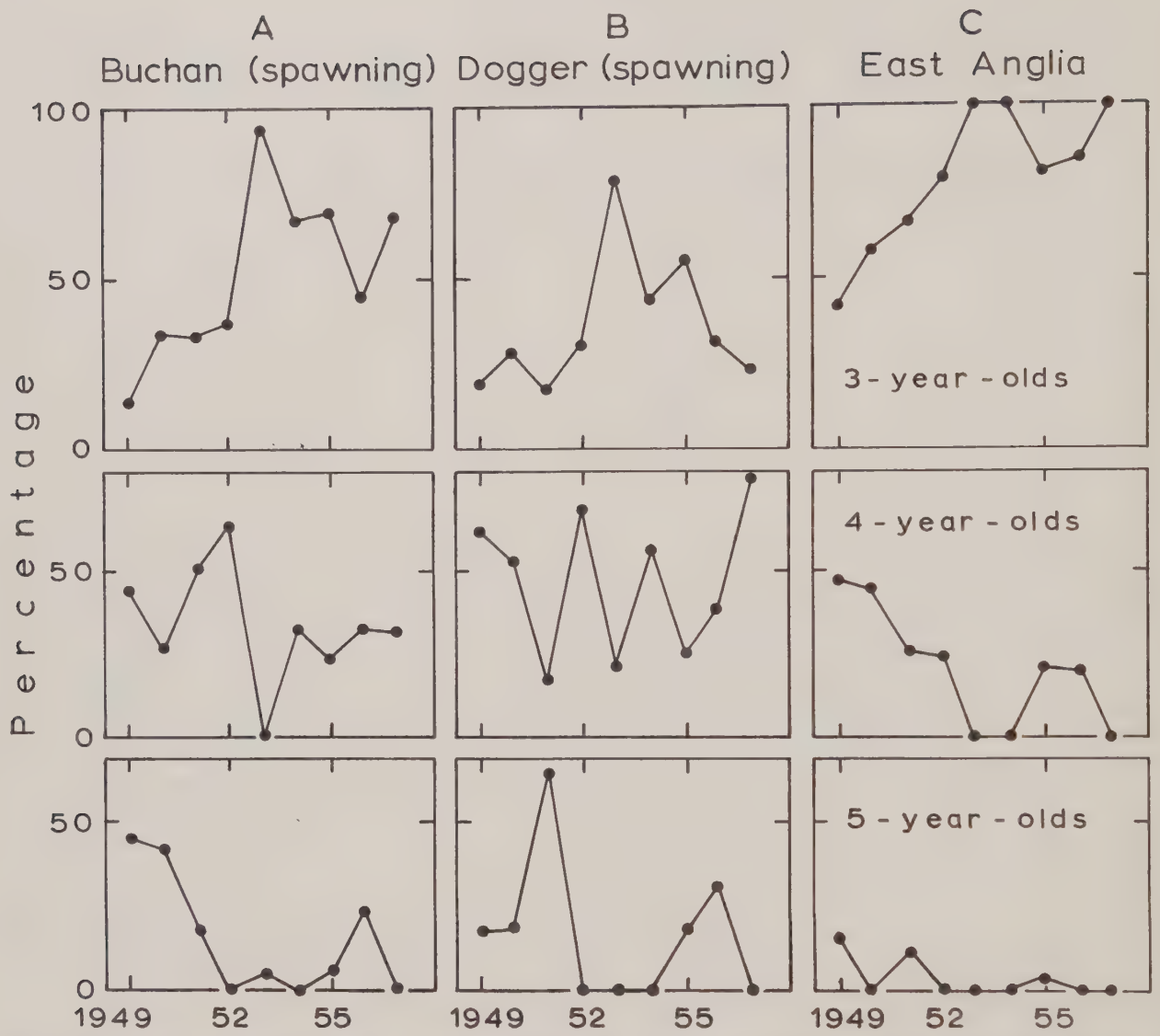

Fig. 8. *The percentage recruitment at three, four and five years of age to the Buchan spawning, Dogger spawning and East Anglian fisheries from* 1949–57.

Sahrhage, 1955; Schubert, 1957, 1958, 1959, 1960). A rougher estimate of recruitment can be made by adding the stock densities (in tons/day) of three- and four-year-old fish for given periods (Figure 10). It is assumed that changes in the pattern of recruitment in the period 1950–2 on the Dogger and on the Fladen were of the same character as those in East Anglia. Both in the Buchan spawning fishery and in the Dogger spawning fishery, partial recruitment can be detected by inspection of the data since 1952. Before the recruitment changes in 1950–2, the sum of stock densities of three- and four-year-olds in age groups is as follows:

Let x be the proportion recruited at three years of age. Then we have

$$x_{n+1}r_3 + (1 \quad x)\, {}_nr_3\, e^{-M} + x\, {}_nr_3\, e^{-Z};$$

where ${}_nr_3$ is the stock density of recruits at three years of age in the year n;

where ${}_{n+1}r_3$ is the stock density of recruits at three years of age in the year $n + 1$.

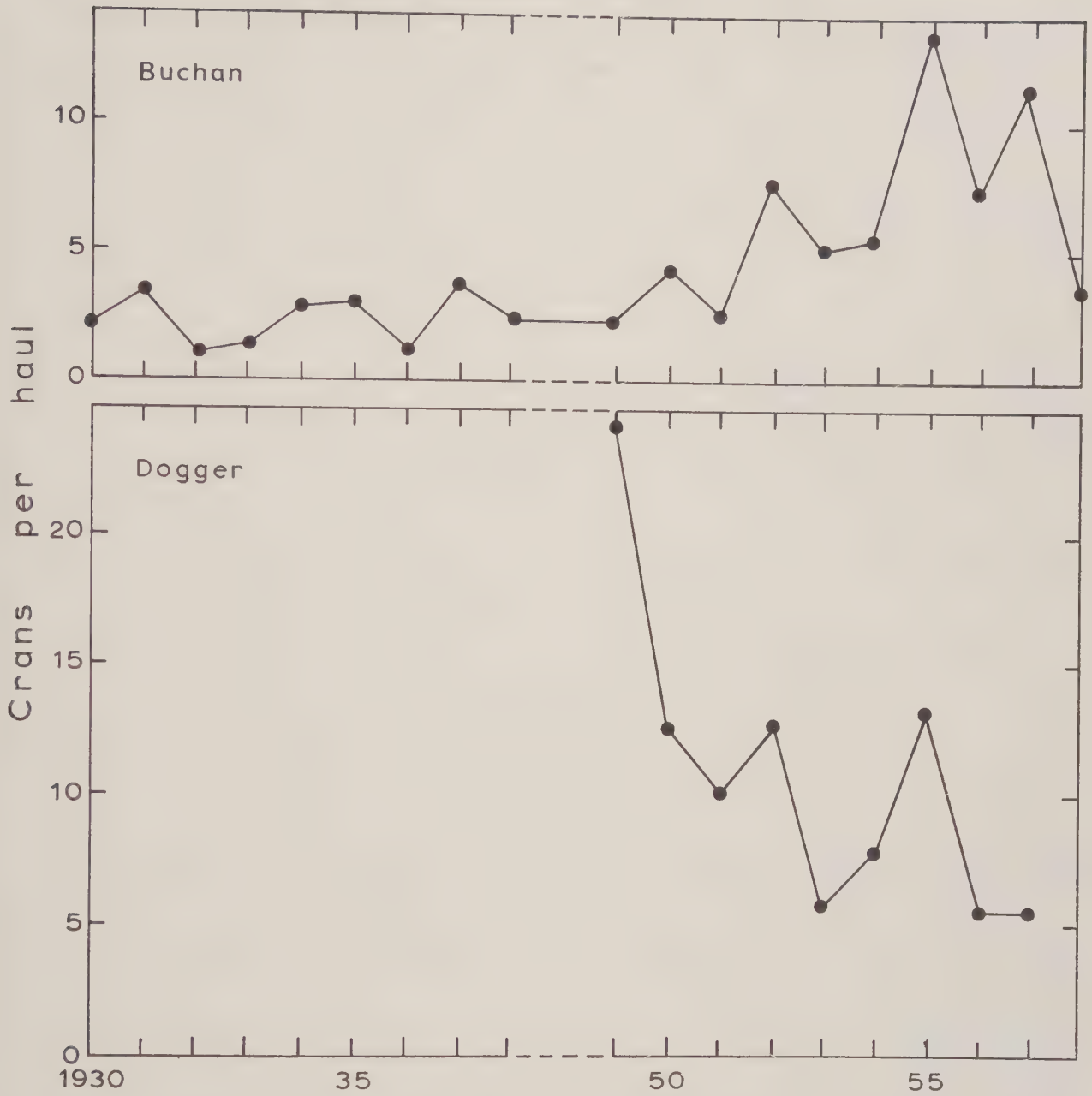

Fig. 9. *Total recruitment to the Buchan spawning fishery (from* 1930–58) *and to the Dogger spawning fishery (from* 1949–57) *in crans per haul as at three years of age.*

In the Dogger fishery it is assumed that $x = 0{\cdot}5$. After the recruitment change, the average of the stock densities of threes and fours in age groups is ${}_{n+1}r_3 + {}_{n}r_3\, e^{-Z}$. If recruitment is steady (or ${}_{n}r_3 = {}_{n+1}r_3$) and M and Z are constant, the ratio of the post-recruitment sum to the pre-recruitment sum is:

$$\frac{r_3\,(1 + e^{-Z})}{0{\cdot}5r_3\,(1 + e^{-M} + e^{-Z})} = \frac{2\,(1 + e^{-Z})}{1 + e^{-M} + e^{-Z}}.$$

Let this formula apply equally to sums of age groups or to sums of year-classes. If $M = 0{\cdot}2$ and Z

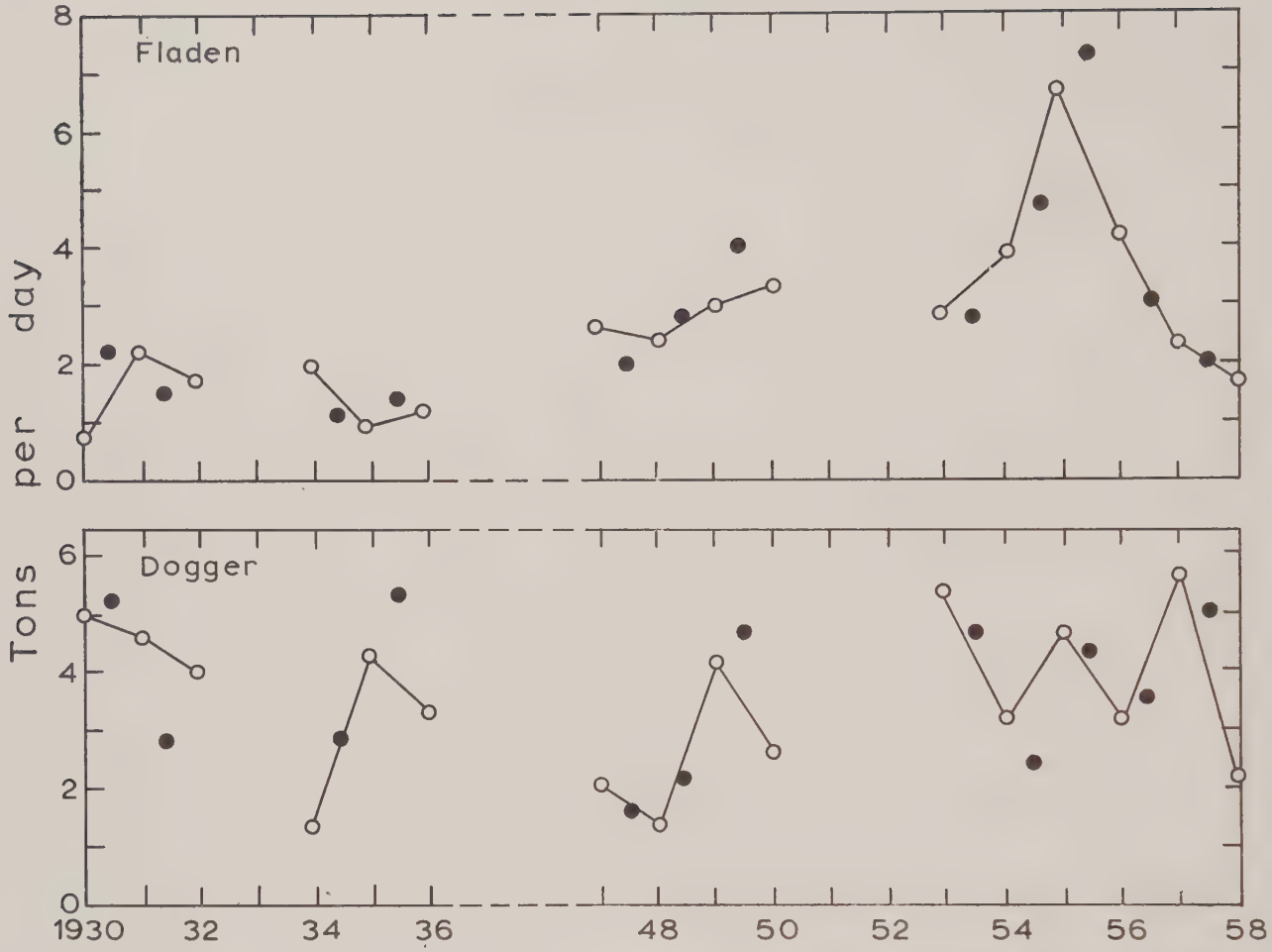

Fig. 10. *Recruitment in tons/day to the Fladen and Dogger fisheries from* 1930–58. *The recruitment is estimated as the sum of three- and four-year-olds in age groups (marked as open circles) and as the sum of three- and four-year-olds in year-classes (marked as solid circles).*

lies between 0·3 and 0·8, an increase after the recruitment change will be expected of 28% ($Z = 0{\cdot}3$) or 32% ($Z = 0{\cdot}8$).

From the character of the age distributions it is likely that the change in recruitment pattern on the Dogger fishery was rather like that at East Anglia. Catches per unit effort (as tons/day) of three- and four-year-old fish have been corrected for the increase in power (Lundbeck, 1959, Table 13), and averaged in age groups for the three periods 1930–6, 1947–50 and 1953–8 as follows:

Period	Age		
	3	4	Σ (3 + 4) (tons per day)
1930–6	1·68	2·12	3·80
1947–50	1·68	1·68	3·36
1953–8	2·32	2·03	4·35

NOTE: The catches per unit effort have been averaged in age groups and not in year-classes, because four observations are gained, making 16 instead of 12 in the period 1930–58.

The increase from 1930–50 to 1953–8 is 21%, which is within that expected for a change in the pattern of recruitment. Hence, we may conclude that the recruitment to the Dogger fishery has been steady between 1930 and 1958, with no upward or downward trend, like that in the uncorrected data for the East Anglian fishery. It will be recalled that the Dogger fishery and the Dogger spawning fishery are being treated separately.

On the Fladen the situation is a little different because in the period 1930–6 only one fifth or less (Cushing, in Burd and Cushing, 1962) of the recruits entered the fishery at three years of age. Then with the formula derived above (let $x = 0{\cdot}2$ for the Fladen fishery) the ratio expected in this treatment is:

$$\frac{r_3 (1 + e^{-Z})}{0{\cdot}2\, {}_{n+1}r_3 + 0{\cdot}8{}_n r_3 e^{-M} + 0{\cdot}2{}_n r_3 e^{-Z}}$$

Let ${}_n r_3 = {}_{n+1}r_3$ and we have $\frac{5 (1 + e^{-Z})}{1 + 4e^{-M} + e^{-Z}}$ as an average ratio, with M and Z constant. With $M = 0{\cdot}2$ and $Z = 0{\cdot}3$, the expected increase in the sum of three- and four-year-olds would be 73·3%; with $M = 0{\cdot}2$ and $Z = 0{\cdot}8$, it would be 53·4%. Using the same treatment as for the Dogger material, we have:

Period	Age		
	3	4	Σ (3 + 4) (tons per day)
1930–6	0·18	1·39	1·57 } 2·41
1947–50	0·83	2·43	3·26 }
1953–8	2·41	1·92	4·33

The increase from 1930–6 to 1947–50 is a doubling. From 1947–50 to 1953–8 there is an increase of 33%, but from 1930–6 to 1953–8 it is 275%. This is more than the increase expected merely because of a change in pattern and it seems that there was an increase in true 'recruitment' between 1930–6 and 1953–8. The increase is shown more clearly in Figure 10 which shows the recruitment to the Fladen and Dogger as a time series. The sums of three- and four-year-old fish in year-classes are also given in the figure. The estimates in year-classes are better than those in age groups, but there are fewer observations. The figure shows more clearly than the tables that recruitment to the Fladen did increase from the thirties up till 1955, independently of any increase in recruitment to the spawning stocks. It also appears that the increase of the recruitment to the Fladen started between 1936 and 1947.

Considering all recruitment changes, the following conclusions seem to emerge:

1. Recruitment to East Anglia, as at three years of age, was apparently steady from 1925–8, with no upward or downward trend in the uncorrected data as used in the other fisheries. It will be shown in Part III that true recruitment has declined since the 1952 year-class.
2. Recruitment to the Dogger spawning fishery, as at three years of age, from 1946–61 (year-classes 1943–58) showed no upward or downward trend.
3. Recruitment to the Buchan spawning fishery, as at three years of age, increased by about three times from 1953 onwards.
4. Recruitment to the more general Dogger fishery (as the sum of three- and four-year-olds in year-classes) was steady from 1930–58, with no upward or downward trend.

5. Recruitment (as the sum of three- and four-year-olds in year-classes) to the Fladen probably started to increase during the war, long before it increased to Buchan spawning fishery and presumably independently of it; a peak was reached in 1955, probably associated with the strong 1952 year-class of Buchan spawners.

The changes in recruit densities have taken place slowly on the Fladen and sharply in the Buchan fishery. This sharp change took place in 1952, at the same time as the growth change and the change in the age of recruitment to the North Sea fisheries. Hence it is likely that this was a true change and not an artefact due to a local increase in efficiency. Further, it is likely that a change in the efficiency of catching did take place in the North Sea fisheries and is shown in the East Anglian fishery (see Part II). The East Anglian fishery showed no sharp increase in stock density in the total recruitment in 1952. Indeed when the effect of the efficiency change is taken into account, it can be shown that the recruitment to the East Anglian fishery has declined sharply.

The Belgian data from the October Dogger fishery include the change in power. The German data on Fladen and Dogger are also corrected for changes in power. Neither the East Anglian data nor the Buchan spawning data are corrected for efficiency changes. The efficiency change amongst the East Anglian driftermen, referred to above, must be associated with changes in searching habits. This form of efficiency change is independent of power and would be to some extent common to trawlers and drifters alike. Herein lies the justification for treating the crude data in the same way throughout the North Sea.

There is a marked contrast between the recruitment patterns, firstly to the Buchan spawning fishery and to the Fladen, and secondly to the Dogger spawning fishery and to the Dogger fishery. The apparent recruitment to the Fladen fishery started to increase long before the sharp increase in recruitment in the Buchan spawning fishery.

In quantities we have for the period 1930–58:

East Anglia:	10 000 to 15 000/shot (where the shots are uncorrected for the efficiency change since 1946);
Buchan spawners:	2 to 12·3 crans/landing;
Dogger spawners:	1·0–4·4 tons/day;
Dogger fishery:	4 tons/day;
Fladen fishery:	1·5–4·5 tons/day.

East Anglian herring weighed on average 140 g during the period; Buchan spawners weighed on average 160 g; a trawler usually catches about two and a half times as much as a drifter. We may retabulate as trawler catch in the early fifties (1952–6):

East Anglia:	3·5–5·5 tons/day;
Buchan spawners:	1·0–5·5 tons/day;
Dogger spawners:	1·0–4·3 tons/day;
Dogger fishery:	4 tons/day;
Fladen fishery:	1·5–4·5 tons/day.

The three latter figures have been corrected for changes in the average power of the trawler fleet. The two former ones are uncorrected although it is known that a change in efficiency has taken place in the East Anglian drifter fleet and (because the same fishermen take part) presumably also in the Buchan spawning fishery.

5. THE ESTIMATION OF THE MIXING OF THE THREE SPAWNING GROUPS IN THE NORTH SEA IN SUMMER AND EARLY AUTUMN

METHOD

It is now fairly well established that samples of the Dogger or Buchan spawners can be distinguished from those of the Downs stock, as discussed above in Section 2, referring particularly to the work of Cushing and Burd (1957), Zijlstra (1958), Baxter (1959) and Muzinic and Parrish (1960). Fish of the Downs stock move into the northern and central North Sea to feed (Krefft, 1954; Burd, in Burd and Cushing, 1962). The problem is to determine the proportions of the Downs stock in the feeding fisheries, and it is assumed (reasonably from Section 2) that the samples of the Downs stock taken at East Anglia represent the single stock which spawns at Sandettié and at Ailly. The essence of the method is to estimate the correlation between the catches per unit of effort at East Anglia and those in a mixed fishery to the north. Any feeding fishery in the northern and central North Sea is potentially a mixture of stocks; the fact that samples of the unmixed Downs stock are available is used to make the separation.

There are three mixed fisheries in the northern North Sea in summer and early autumn: the Buchan pre-spawning fishery, the Shetland fishery, and the Fladen fishery. In the central North Sea there is a series of fisheries from the Farne Deep, North East Bank and the Gut to Whitby and the grounds around the Dogger Bank itself; some of these grounds are spawning grounds, but on others it is likely that East Anglian fish mix in some proportion. The evidence on this point was summarized in an earlier section.

The method used is to correlate catches/effort of age groups in a spawning fishery with those in a mixed fishery. The correlation estimates the extent of the occurrence of the spawning fish in the mixed fishery and the degree of intrinsic year-class association between the two groups.

In order to use the catches/effort of all age groups, thus increasing the quantity of information, factors correcting for mortality between age groups and for abundance between years were calculated. There is an array of stock densities, y, by age and by years, in one fishery:

The row ${}_1y_3, {}_1y_4 \ldots {}_1y_{n_1}$ represents the first year's densities by age, n_1 being the last age group;

The column ${}_1y_3, {}_2y_3 \ldots {}_{n_2}y_3$ represents the densities of age 3 by years, n_2 being the number of years.

Mean densities are calculated for each row and each column:

${}_1\bar{y}, {}_2\bar{y} \ldots {}_{n_2}\bar{y}$ represent mean densities for each year;

$\bar{y}_3, \bar{y}_4 \ldots \bar{y}_{n_1}$ represent mean densities for each age.

The overall mean density is $\bar{y}$.

The correction factor for mortality is, for example, for three-year-olds: $\bar{y}/\bar{y}_3$.

The correction factor for abundance, is, for example, for the first year: $\bar{y}/{}_1\bar{y}$.

Each item is corrected by two factors, one for mortality and one for abundance; for example for three-year-olds in the first year:

$$ {}_1y_3 \cdot \bar{y}/\bar{y}_3 \cdot \bar{y}/{}_1\bar{y}. $$

In this way, differences between age groups due to mortality are minimized, as are differences between years due to trends in abundance.

There is an array representing the stock densities in the mixed fishery, y, and an array representing those in the unmixed fishery, x, for the same period of years and the same set of ages. The pairs of stock densities, corrected for mortality and abundance, are correlated. The regressions, $y = a + bx$ and $x = a' + b'y$ are calculated. An example of the full calculation made is given: the correlation between the Buchan spawning fishery (x) and the Shetland fishery, 1930–9 (y).

The basic data used are the catches/effort (as tenths of crans) of each age group in the Buchan spawning and Shetland fisheries from 1930 to 1939 (Parrish and Craig, 1964). They are given in Table 5.

Table 5. *Stock densities (tenths of crans) of each age group from 3 to 9, in the Buchan spawning fishery and in the Shetland fishery.*

Buchan spawning fishery (August–September)

	Ages							
	3	4	5	6	7	8	9	Σ
1930	6·2	16·0	12·0	8·0	6·9	7·9	3·8	60·8
1931	7·8	9·7	6·5	5·4	3·9	3·9	3·1	40·3
1932	5·6	33·0	8·0	4·3	1·8	1·4	0·9	55·0
1933	11·0	23·0	45·0	6·5	7·6	5·9	3·3	102·3
1934	2·9	10·0	19·0	62·0	11·0	9·7	5·7	120·3
1935	8·1	33·0	10·0	16·0	27·0	3·8	4·4	102·3
1936	0·9	13·0	18·0	8·9	15·0	21·0	6·6	83·4
1937	2·0	3·3	18·0	14·0	2·5	3·9	12·0	55·7
1938	17·0	32·0	7·8	9·8	7·3	2·6	2·0	78·5
1939	14·0	11·0	7·6	2·2	3·2	2·3	1·1	41·4
Σ	75·5	184·0	151·9	137·1	86·2	62·4	42·9	740·0

Shetland fishery (May to July)

	Ages							
	3	4	5	6	7	8	9	Σ
1930	33·0	33·0	40·0	47·0	8·9	15·0	8·9	185·8
1931	7·4	47·0	10·0	12·0	14·0	10·0	8·7	109·1
1932	0·6	58·0	42·0	12·0	7·4	10·0	5·2	135·2
1933	2·7	13·0	30·0	15·0	6·4	3·7	5·7	76·5
1934	0·9	64·0	28·0	44·0	15·0	5·6	2·6	160·1
1935	16·0	44·0	39·0	35·0	32·0	11·0	4·8	181·8
1936	0·4	28·0	43·0	23·0	19·0	22·0	6·0	141·4
1937	—	15·0	43·0	47·0	16·0	8·6	33·0	162·6
1938	—	13·0	15·0	36·0	28·0	25·0	18·0	135·0
1939	0·9	5·3	29·0	12·0	17·0	8·7	3·7	76·6
Σ	61·9	320·3	319·0	283·0	163·7	119·6	96·6	1 364·1

The correction factors are given in Table 6. Those for the three-year-olds in the first year in the Shetland fishery are:

$$\bar{y}/\bar{y}_3 \text{ (for mortality)} = 3{\cdot}148$$

$$\bar{y}/{}_1\bar{y} \text{ (for abundance)} = 0{\cdot}734$$

Similarly for the Buchan spawning fishery they are:

$$\bar{y}/\bar{y}_3 \text{ (for mortality)} = 1{\cdot}400$$
$$\bar{y}/{}_1\bar{y} \text{ (for abundance)} = 1{\cdot}217.$$

Table 6. *Correction factors for the correlation of stock densities in the Buchan spawning fishery and in the Shetland fishery,* 1930–9

Correction factors for mortality

Age	Buchan spawners	Shetland
3	1·400	3·148
4	0·575	0·608
5	0·696	0·611
6	0·771	0·689
7	1·226	1·190
8	1·694	1·629
9	2·464	2·017

Correction factors for abundance

	Buchan spawners	Shetland
1930	1·217	0·734
1931	1·836	1·250
1932	1·345	1·009
1933	0·723	1·783
1934	0·615	0·852
1935	0·723	0·750
1936	0·887	0·965
1937	1·329	0·839
1938	0·843	1·810
1939	1·787	1·781

Regressions were calculated for each age group in the time series and for all the data. In this case no regression was significantly different from zero save that using all the data [$p = 0{\cdot}01$; $(1 - a'/\bar{x})100 = 27{\cdot}9\%$ and $(1 - a/\bar{y})100 = 31{\cdot}3\%$.] No difference was found between the sums of squares, taken individually, and the total sums of squares ($F = 1{\cdot}4$; $n = 56$); so it is unlikely that the regression using all the data was biased by any single regression, for one age group. The combined data are illustrated in Figure 15. The intercept is $13{\cdot}89$ ($\bar{x} - 19{\cdot}27$) $\pm$ $5{\cdot}2$; in $(1 - a'/\bar{x})100$ the confidence limits (at 95%) to the value of $27{\cdot}9\%$ are 1%–55%.

There are two possible sources of error in this procedure. The first is a bias that is found when the shape of an age distribution changes over a time period, as for example during the recruitment change of 1950–2. The effect is to make, for example, $\bar{y}_3$ and ${}_1\bar{y}$ larger than they should be and so the corrected age distribution becomes biased. The presence of the bias in the corrected terms can be found by detecting a significant trend with time in an age group. In general, the bias is eliminated by separating the series before the recruitment change from that after it.

The second possible error, affecting tests of significance of regressions, is that perhaps the corrected data, being derived from catches per unit effort, are not normally distributed. For some age distributions in corrected data in the East Anglian fishery, the Buchan spawning fishery, the Belgian Dogger

fishery, the Shetland fishery and the Fladen fishery, no correlation was detected between mean and variance. Hence no transformation is necessary.

In Part III, it will be shown that by the time that the 1959 year-class had entered the fishery, recruitment to the Downs stock had declined by nearly three times. If true recruitment declines, then presumably the mixing rate declines. As decline became noticeable with the 1955 year-class in 1958, we would expect mixing rates to diminish, using data uncorrected for the efficiency change. The proportion of Downs fish on Fladen, estimated by the maturity stage technique, was 50% from 1950–4, but fell to 19% in 1955–9. This may in part have been due to an increased proportion of Buchan spawners, but it is the sort of result that might be expected as the Downs stock started to decline in 1955–9. It is thought that during the decade of the fifties, the decline was not great enough to reduce the average value very much. However, it must be obvious that if the technique were used in the decade 1955–65, it might yield an insignificant value, merely because the Downs stock was very low as compared with the other two stocks.

In the section on recruitment (Section 4), it was pointed out that recruitment to the Buchan spawning stock had increased during the fifties. German and Belgian trawl data on herring catches have been corrected for changes in power. Further, changes in efficiency have been detected in the East Anglian data. All these trends with time appear as changes in apparent abundance, and it was to minimize such changes that the correction for abundance was used. Then the catch per unit effort data were uncorrected for efficiency changes in East Anglia or in the Buchan and Shetland drift-net fisheries and uncorrected for power changes in the German Dogger and Fladen fisheries. The Belgian age distributions during the fifties in the October Dogger fishery were used as 'kg/100 hp × voyages', because the power factor could not be eliminated from the published distributions. It is thought that a trend in apparent abundance due to power changes will be minimized by the corrections for abundance and that the scalar differences (due to differences between true and apparent abundance between two stocks) in the correlations do not matter.

In the material used, there are gaps in the time series because not all the fisheries examined have been sampled in all years. In the subsequent treatment many regressions of individual age groups in the original data are not significantly different from zero. When the age groups are combined into an array of corrected terms as shown above, correlation between fisheries may emerge merely because a greater quantity of information has been used. The question arises whether the regressions in combined data are generated merely in the use of the correction terms. This point can be tested; the sums of squares about regression are added for each age and are divided by the number of degrees of freedom available to the individual regressions. This mean square is compared (by means of an F test) with the mean square for the pooled regressions for all ages. No difference was found in any of the correlations to be used, and so no regression of an individual age group is sufficiently different to bias the regressions of data combined from all age groups.

The correlation is composed of two regressions, $y = a + bx$ and $x = a' + b'y$, where y is the stock density of the mixed stock and x that of the single stock. The first regression estimates the dependence of the single stock on the mixed stock; the intercept estimates that part of the single stock which does not reach the mixed stock. The second regression estimates the dependence of the mixed stock on the single stock; then $(1 - a'/\bar{x})100$ is the proportion of the mixed stock composed of the single stock. The latter is the estimate of mixing rate that will be used in the first place.

In a later section (5), on the estimation of mixing from the use of maturity stage distributions in the mixed fisheries, $(1 - a/\bar{y})100$ will be used. Here y represents the mixed stock in a given maturity stage and x represents the single stock. The intercept represents that part of the stock in maturity stage V which is independent of the pure stock. So $(1 - a/\bar{y})100$ represents that part of the pure stock present in the mixed fishery.

MATERIAL

1. *The spawning groups*
   a. East Anglian fishery 1930–8, 1946–60; ages 3–8.
   b. Belgian October Dogger fishery 1949–59; ages 3–9 (Gilis, 1957, 1958, a, b, c, 1959, 1961).
   c. Buchan spawning fishery 1930–8, 1948, 1950–60; ages 3–9 (Parrish and Craig, 1964).
2. *The mixed fisheries*
   a. Buchan pre-spawning fishery, 1930–8, 1947, 1948–60; ages 3–8 (Parrish and Craig, 1964).
   b. Shetland fishery, 1930–8, 1948–60; ages 3–9 (Parrish and Craig, 1964).
   c. Fladen fishery, 1930–2, 1934–6, 1946–50, 1953–60; ages 3–9 (Krefft, Schubert and Sahrhage, 1955; Schubert, 1957, 1958, 1959, 1960, 1962).
   d. Dogger fishery, 1930–2, 1934–6, 1946–50, 1953–60; ages 3–9 (Krefft, Schubert and Sahrhage, 1955; Schubert, 1957, 1958, 1959, 1960).

RESULTS

1. THE NATURE OF YEAR-CLASS CORRELATION BETWEEN THE SPAWNING GROUPS

The character of recruitment to the three spawning groups was discussed in an earlier section. It will be recalled that the data (in stock density uncorrected for the efficiency change) showed no upward or downward trend in recruitment to the East Anglian fishery (1925–58). There has been no upward or downward trend in the recruitment to the Dogger spawning fishery (Herring Assessment Group Report, 1964). Recruitment to the Buchan spawning fishery increased by about three times from 1953 onwards. To the general Dogger fishery, there was no trend of 'recruitment' (as sum of three- and four-year-olds) from 1930–58. There was a slow increase in 'recruitment' (as sum of three- and four-year-olds) to the Fladen fishery, probably starting during the war, some time before the dramatic increase to the Buchan spawning fishery.

To estimate the year-class correlation between the spawning groups, the total recruitment as at three years of age should be used over as long a period as possible. Figure 11 shows the relationship in total recruitment between: the East Anglian fishery and the October Dogger fishery from 1949–59; the October Dogger fishery and the Buchan spawners from 1949–59; and the East Anglian fishery and the Buchan spawning fishery from 1930–8 and from 1949–60. In no case is there any correlation; nor is there any correlation between the East Anglian fishery and the Buchan spawning fishery for the two periods combined, 1930–60. The figure also shows the relationships for three-year-olds, four-year-olds and the sum of threes and fours; again no correlation is found. Hence we may say that there is no year-class correlation between any of the three spawning groups, at any age, if taken separately.

In the overall examination of the original data it was found that negative regressions sometimes occurred. Between East Anglia and Shetland, there is a negative regression amongst the four-year-old fish from 1930–48; for the same period there is one between East Anglia and Fladen for four-year-old fish (Figure 12A). There is none between East Anglia and the Buchan pre-spawning fishery at four years of age in the period before the recruitment change. Hence there is a difference between the Buchan pre-spawning fishery on the one hand and the Shetland and Fladen fisheries on the other. In the period after the recruitment change, a negative regression (in three-year-old fish) is found only in the relationship between East Anglia and Fladen (Figure 12B). The main biological difference between the two periods is the increase in Buchan spawning stock after the recruitment change. It will be shown below that most of the recruiting fish going to Shetland after the recruitment change

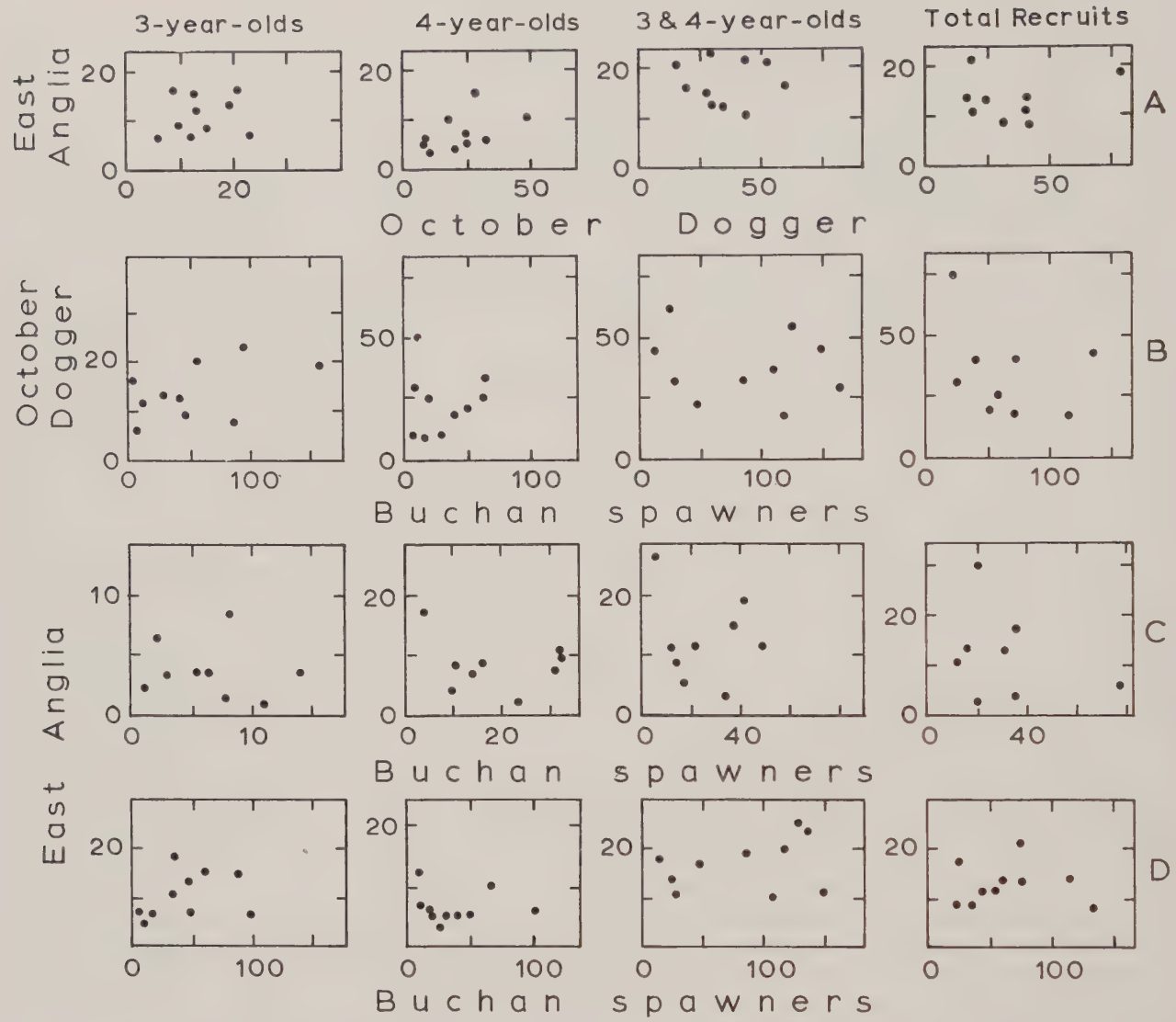

Fig. 11. *Recruitment correlations between the spawning groups; column* 1, *three-year-olds; column* 2, *four-year-olds; column* 3, *the sum of three- and four-year-olds; column* 4, *total recruitment as at three years of age.* A. *East Anglia on October Dogger,* 1949–59; B. *October Dogger on Buchan spawners,* 1949–59; C. *East Anglia on Buchan spawners,* 1930–8; D. *East Anglia on Buchan spawners,* 1949–60. *In no case is any correlation significantly different from zero.*

were Buchan spawners. It is suggested that the negative correlation found at four years of age between East Anglia and Shetland was destroyed as Buchan spawners became a dominant component at Shetland. A negative year-class correlation, however, is possible; Popp Madsen's method (1960) of predicting the recruitment to the East Anglian fishery is an inverse correlation of high modal length on the Bløden ground with the magnitude of recruitment in catch per effort of three-year-old fish to the East Anglian fishery. Such a relationship might yield a negative correlation between East Anglian recruits and the sum of Buchan and Dogger recruits.

There are three groups of compound year-class correlations. There is no correlation of Buchan on 'East Anglia plus Dogger', of Dogger spawners on 'East Anglia plus Buchan', or of East Anglia on 'Buchan plus Dogger' spawners in total recruitment. In the data combined from all age groups a

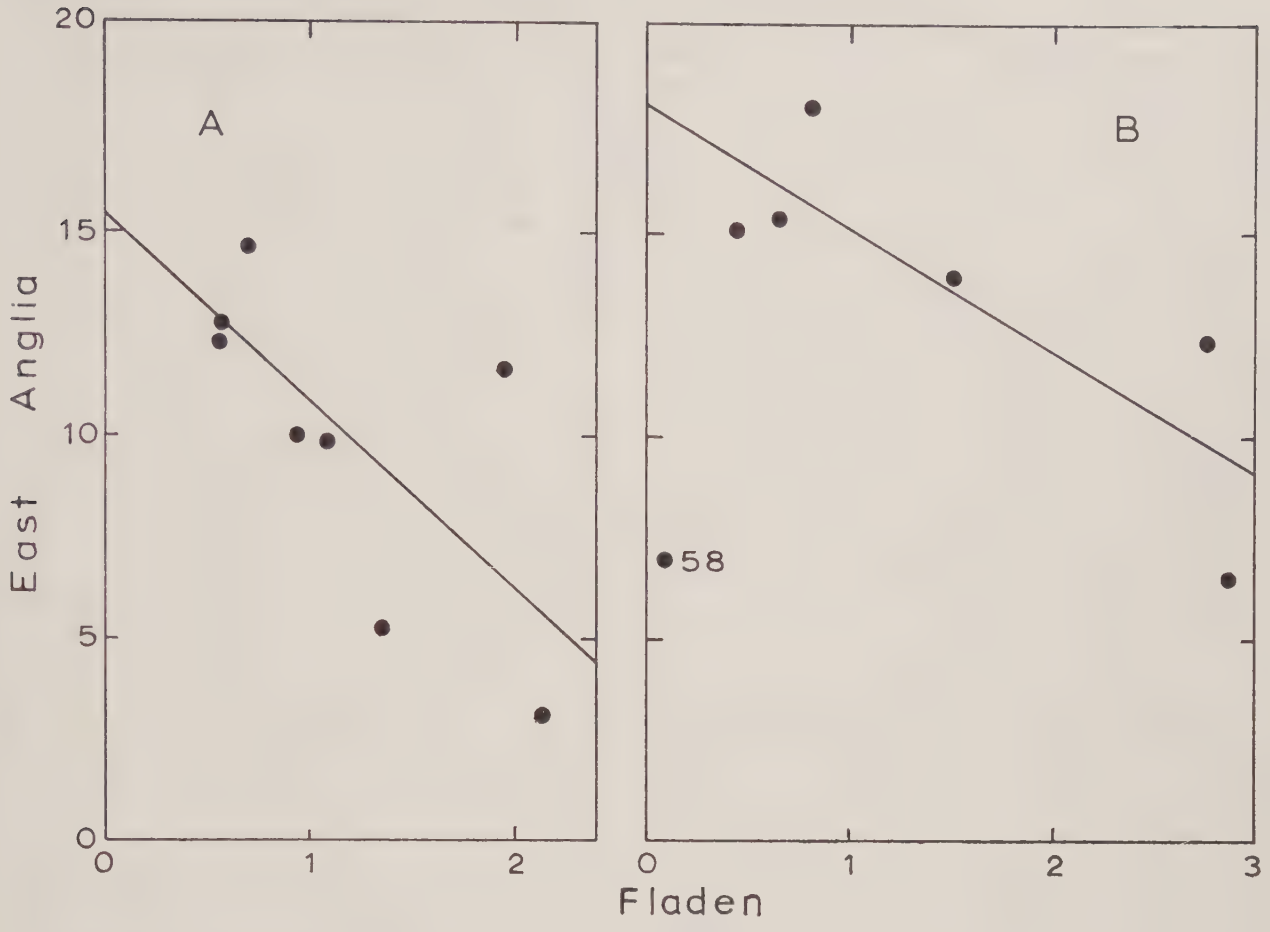

Fig. 12. *Regression of four-year-olds at East Anglia on the same on the Fladen,* 1930–48 (*A*) *and of three-year-olds at East Anglia on the same on the Fladen,* 1953–9 (*B*).

negative and significant regression is found between the East Anglian data and the Fladen for the period 1953–8; in the original data during this period there are negative regressions for the three-year-olds, four-year-olds and six-year-olds. This is what would be expected if there was a negative year-class correlation between the East Anglian catches/effort and the sum of the Dogger and Buchan catches per effort. Hence, it is likely that the negative correlation of East Anglia on Fladen found in the combined data was generated by year-class correlation of the nature found between East Anglia and the sum of Buchan and Dogger spawners.

In no other combination can any form of year-class correlation be detected. For the subsequent treatment this is a valuable conclusion; if the only year-class correlation to be detected is negative, then a positive correlation found in the combined data must be due to mixing only, and the degree of mixing as calculated by the above method is an underestimate.

2. THE ESTIMATES OF MIXING FROM THE COMBINED DATA

(i) *The Buchan spawners in the mixed fisheries*

In this section are given the final correlations only. Figure 13A shows the correlation in the combined data between the Fladen and the Buchan spawning fishery for the period 1930–47. The data are separated into two parts, recruits (ages three and four) and older fish (ages five to nine).

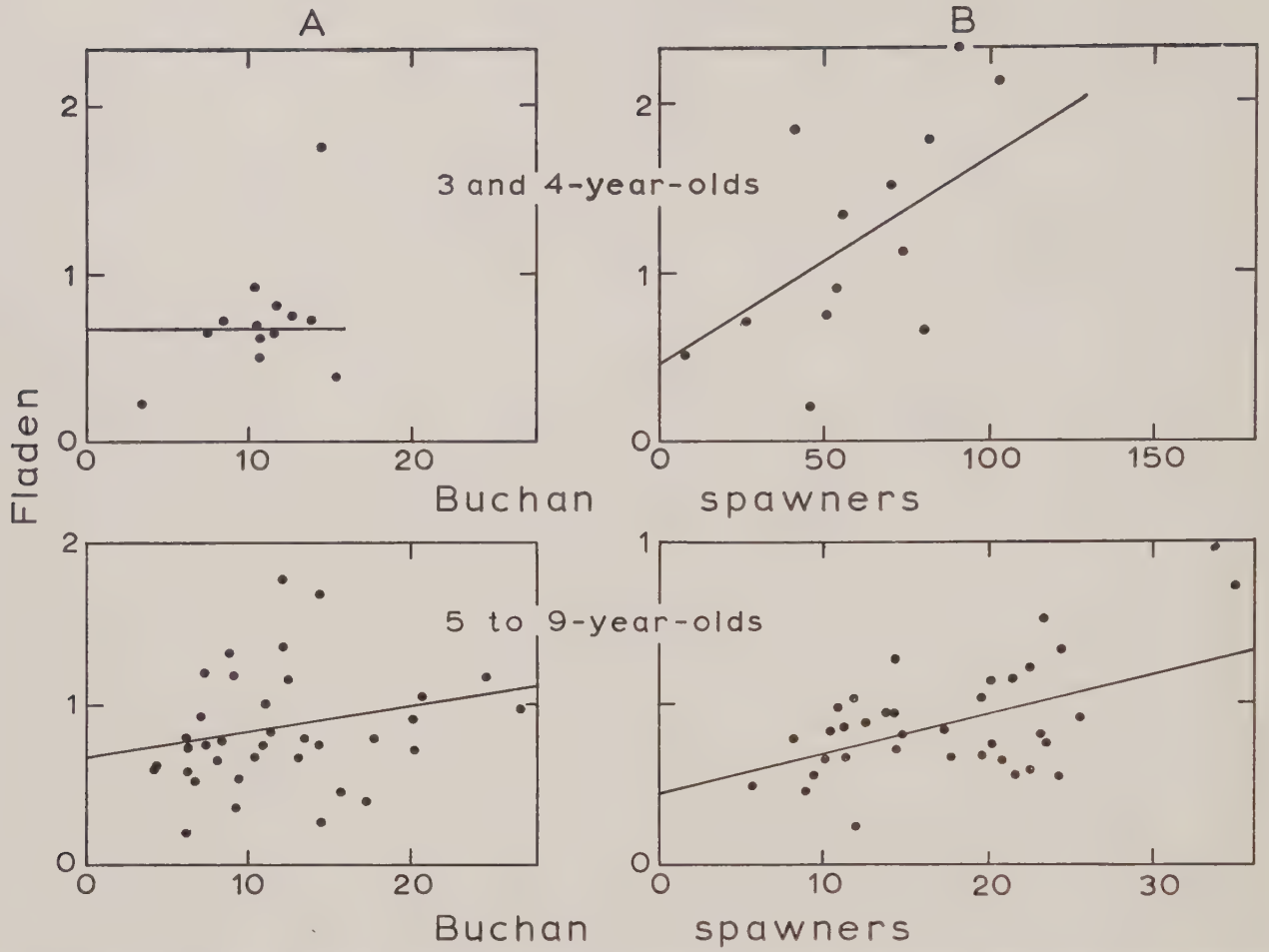

Fig. 13. *Regressions of stock densities, corrected for mortality and abundance, on the Fladen on the same in the Buchan spawning fishery. The data are shown separately for the ages three and four and for the ages five to nine.* A. *For the period* 1930–47 (1930–2, 1934–6, 1947)*; neither regression is significantly different from zero.*
B. *For the period* 1953–9*; both regressions are significantly different from zero.*

Neither correlation is significantly different from zero, but that for the older fish has a positive slope. In the combined data for the period 1953–9 (Figure 13B), there is a significant correlation (r = 0·69**) in the ages three and four, and also (r = 0·48**) for the older ages, five to nine. An arrangement closer to the original data is to separate the ages three, four and five from those of six, seven and eight; that for the younger fish is significant (r = 0·69**), but that for the older fish is not (r = 0·23). From the analysis of partial recruitment to the Buchan spawning fishery given above (Section 4) it is possible that recruitment continues up to five years of age. From the data given here it appears that before the recruitment change of 1950 the Buchan spawners did not comprise a significant part of the Fladen stock; after the change, however, the younger fish on the Fladen probably comprised a significant proportion of Buchan spawners. The estimates of $(1 - a'/\bar{x})100$ (the measure of the mixing of Buchan spawners in the Fladen fishery) are:

	1930–47	1953–9
ages 3, 4, 5	Not S	74% (r = 0·69**) (ages 3, 4, 5 only)
ages 6–9	Not S	

** Indicates correlation coefficient significant at p = 0·01.
* Indicates correlation coefficient significant at p = 0·05.

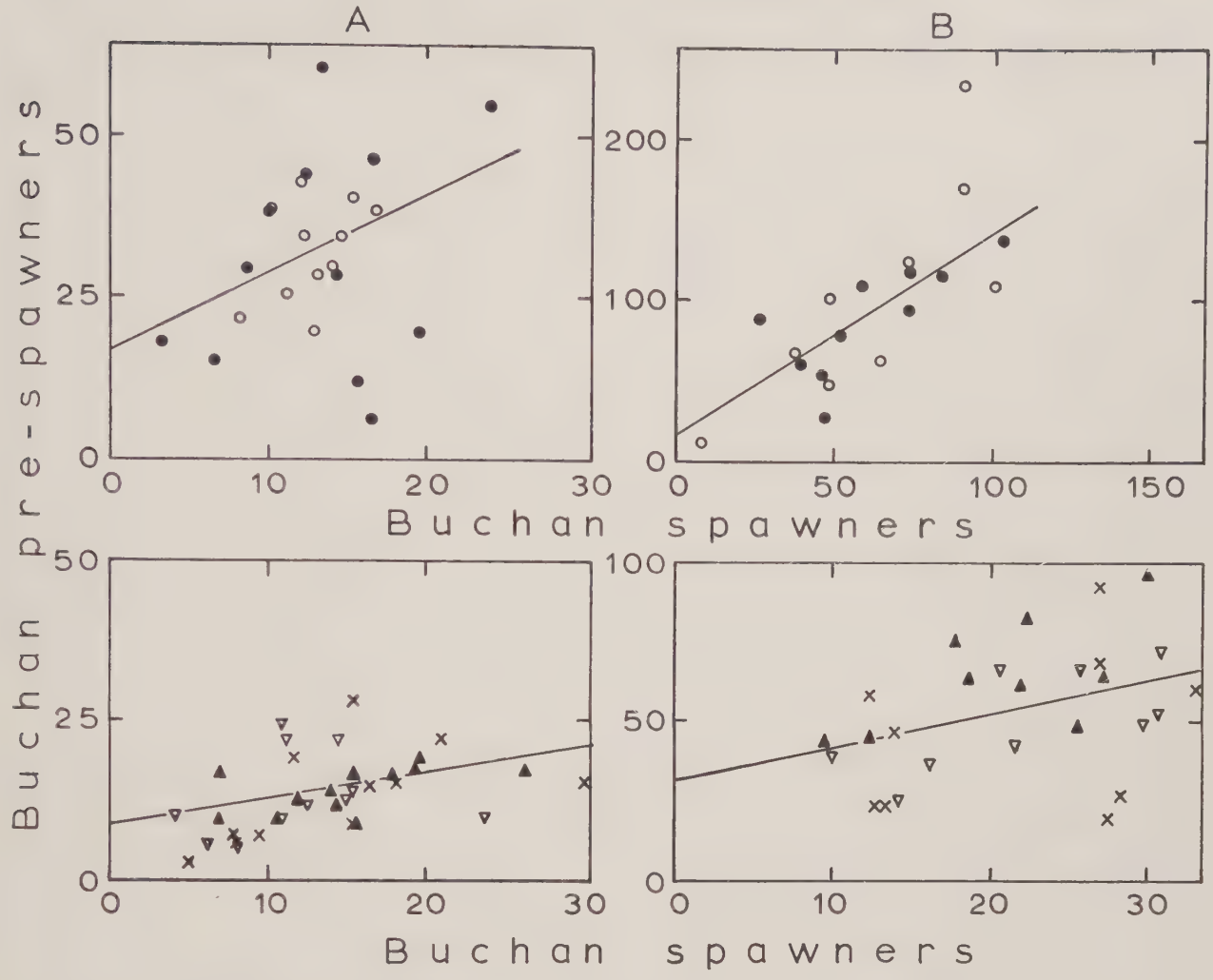

Fig. 14. *Regressions of stock densities, corrected for mortality and abundance, in the Buchan pre-spawning fishery on the same in the Buchan spawning fishery. Above: regressions for the ages three (●) and four (○); below: regressions for the ages five (▲), six (▽), and seven (×).* A. *For the period* 1930–47*; both regressions are significantly different from zero.*
B. *For the period* 1952–60*; both regressions are significantly different from zero.*

In Figure 14 is given the relationship between the Buchan pre-spawning fishery and the Buchan spawning fishery. For the period 1930–47, in Figure 14A, the correlations are separated into that for three- and four-year-olds ($r = 0{\cdot}40^*$), and that for the fives, sixes and sevens ($r = 0{\cdot}43^*$). Figure 14B shows the combined data in the period 1952–60, for the threes and fours ($r = 0{\cdot}67^{**}$) and the fives, sixes and sevens ($r = 0{\cdot}40^*$). There is a significant correlation for the older fish and the recruits both before and after the recruitment change. The estimates of $(1 - a'/\bar{x})100$ are:

	1930–47	1952–60
ages 3, 4	43% ($r = 0{\cdot}40^*$)	79% ($r = 0{\cdot}67^{**}$)
ages 5, 6 7	40% ($r = 0{\cdot}43^{**}$)	40% ($r = 0{\cdot}40^*$)

Figure 15 shows the relationship between the Buchan spawning fishery and the Shetland fishery for all ages (3–9); there is a significant correlation coefficient ($r = 0{\cdot}30^*$) for the period 1930–9; for the

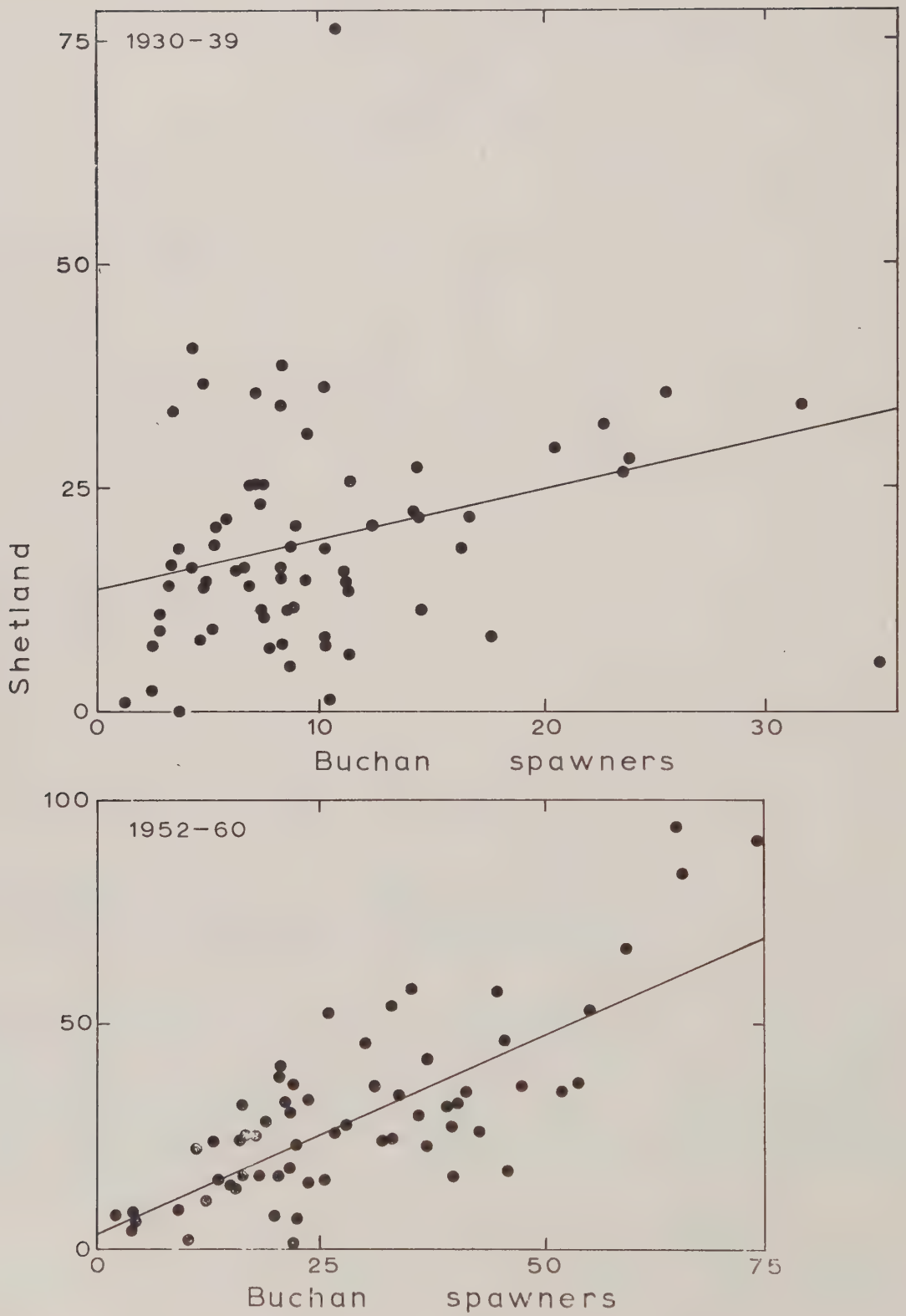

Fig. 15. *Regressions of stock densities of all age groups from* 3 *to* 9, *corrected for mortality and abundance, in the Shetland fishery on the same in the Buchan spawning fishery, for the period* 1930–9, *and separately for the period* 1952–60.

later period, 1952–60, the correlation coefficient for the combined data for all ages (3–9) is also significant ($r = 0{\cdot}77^{**}$). The estimates of $(1 - a'/\bar{x})100$ (the measure of the mixing of Buchan spawners in the Shetland fishery) are:

	1930–9	1952–60
ages 3–9	28% ($r = 0{\cdot}30^{*}$)	79% ($r = 0{\cdot}77^{**}$)

In terms of the correlation technique, the older Buchan spawners were absent on the Fladen ground in the pre-war period, probably present at all ages in the Buchan pre-spawning fishery and perhaps present at all ages in the Shetland fishery. After the recruitment change in 1950–2, it is likely that the Buchan stock increased by about three times. Subsequently, it is likely that many of the recruits on the Fladen ground were Buchan spawners, but the older fish were still not found there. In the Buchan pre-spawning fishery during the period 1952–60 the same sort of correlation was found, marked amongst recruits and less so amongst the older fish. In the Shetland fishery it is likely that the Buchan spawners have predominated in the later period. Hence, before the recruitment change the Buchan spawners were perhaps present in all three mixed fisheries, but never predominantly so. After the recruitment change the Buchan spawners probably became dominant in the Shetland fishery and were found in fair proportions amongst the recruits to the Buchan pre-spawning fishery and to the Fladen. With the use of this technique, it appears that the older Buchan fish are not present in the Buchan pre-spawning fishery and on the Fladen.

(ii) *The October Dogger spawners in the mixed fisheries*

The next series of figures concerns the October Dogger fishery. Data are available only from 1949 to 1959 and so a bias was not introduced at the time of the recruitment changes. Figure 16 shows the correlations in the combined data between the October Dogger spawners and the Buchan pre-spawning fishery. For the recruit fish (three and four years of age, Figure 16A), the correlation is high ($r = 0{\cdot}64^{**}$); that for the older fish (five to eight years of age, Figure 16B) is a little less ($r = 0{\cdot}56^{**}$). On the Fladen ground (Figure 16C) there is a high correlation for the combined data for all ages ($r = 0{\cdot}59^{**}$); for the three- and four-year-old fish only, the correlation coefficient ($r = 0{\cdot}80^{**}$) is a little higher than that for the older fish (ages 5–8, $r = 0{\cdot}63^{**}$). In the Shetland fishery (Figure 16D), $r = 0{\cdot}35^{*}$ for all ages, 5–8 combined; the recruits were excluded after inspection of the original data. The estimates of $(1 - a'/\bar{x})100$ are:

Ages	Buchan pre-spawning fishery	Shetland	Fladen
	1949–59	1949–59	1953–59
3–4	65% ($r = 0{\cdot}64^{**}$)	—	—
5–8	54% ($r = 0{\cdot}56^{**}$)	24% ($r = 0{\cdot}35^{*}$)	—
3–8	—	—	59% ($r = 0{\cdot}59^{**}$)

The results from the examination of the October Dogger correlations suggest that a significant proportion of recruits and older fish in the Buchan pre-spawning fishery are October Dogger spawners. Similarly, October Dogger recruits and older fish comprise a significant proportion of the Fladen fishery. In the Shetland fishery, the older Dogger spawners are present, but probably in small proportion. These conclusions are not surprising, putting in different form what might have been expected from a knowledge of the general biology of the region.

(iii) *The Downs spawners (as sampled in the East Anglian fishery) in the mixed fisheries*

We consider firstly the relation between the East Anglian stock and the Buchan spawners from 1930 to 1955; the correlation is not significantly different from zero (Figure 17). As it is thought that

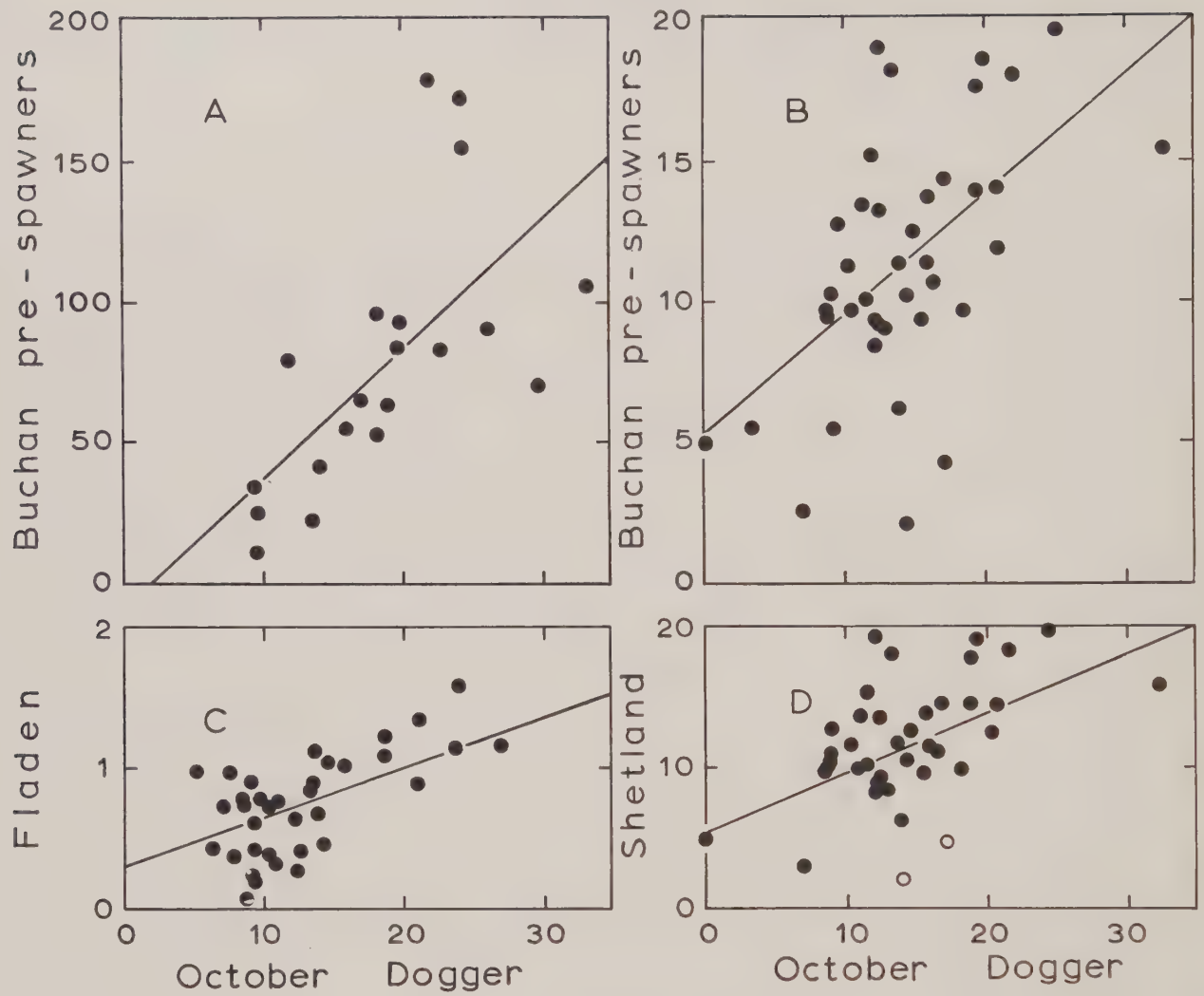

Fig. 16. A. *Regression of stock densities, corrected for mortality and abundance, of three- and four-year-old Buchan pre-spawners on the same in the October Dogger fishery, for the period* 1949–59*; the regression is significantly different from zero.*
B. *The same as Figure* 16*A, for the ages five to eight; the regression is significantly different from zero.*
C. *Regressions of stock densities, corrected for mortality and abundance, of fish aged three to eight, on the Fladen on the same in the October Dogger fishery, for the period* 1953–9*; the regression is significantly different from zero.*
D. *Regressions of stock densities, corrected for mortality and abundance, of fish aged five to eight, at Shetland on the same in the October Dogger fishery, for the period* 1949–59*; the regression is significantly different from zero. The two points marked as open circles may have been biased downwards in the correction procedure.*

the adult spawners return to the same spawning ground year after year, during their adult lives (see Section 2), such a conclusion is not unexpected. Figure 18 shows the relation between the East Anglian stock and the Shetland fishery, for the ages 3–9, in the period 1930–55; there is a slight positive correlation which is not significant. It will be recalled that no fish tagged in Shetland have been recovered in the Southern Bight. In Figure 19 is given the relationship between the East Anglian stock and the Fladen stock. In the combined data (Figure 19A), there is a positive correlation for all ages (3–9) for the early period, 1930–50 (r = 0·27*); but in the later period 1953–8, for the combined data (Figure 19B), for ages 3 and 4–6, there is the negative correlation (r = −0·26*) referred to in Section 3.

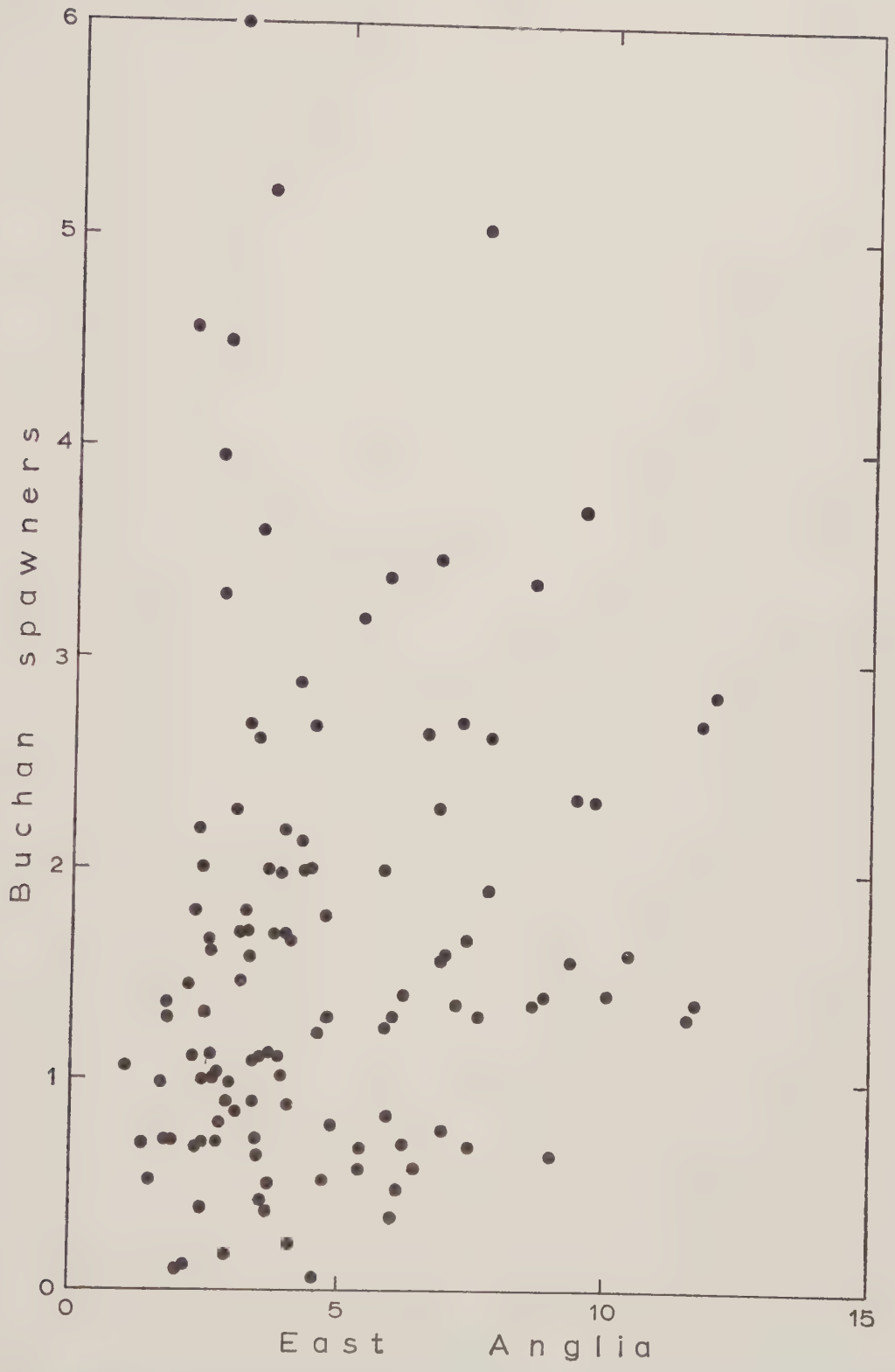

Fig. 17. *Regression of stock densities, corrected for mortality and abundance, of Buchan spawners and East Anglian fish, aged three to nine, for the period* 1930–55*; the regression is not significantly different from zero.*

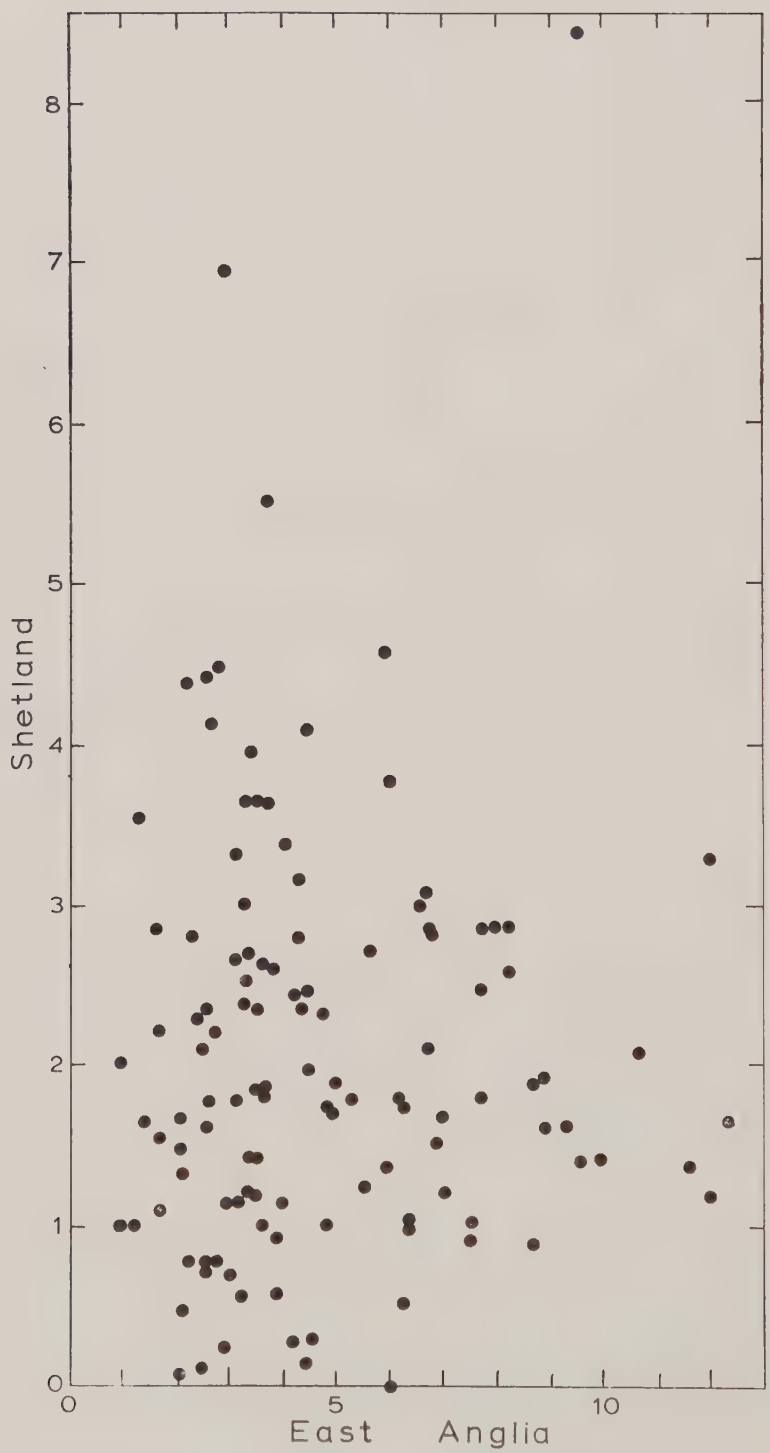

Fig. 18. *Regression of stock densities, corrected for mortality and abundance, of Shetland fish and East Anglian fish, aged three to nine, in the period* 1930–55*; the regression is not significantly different from zero.*

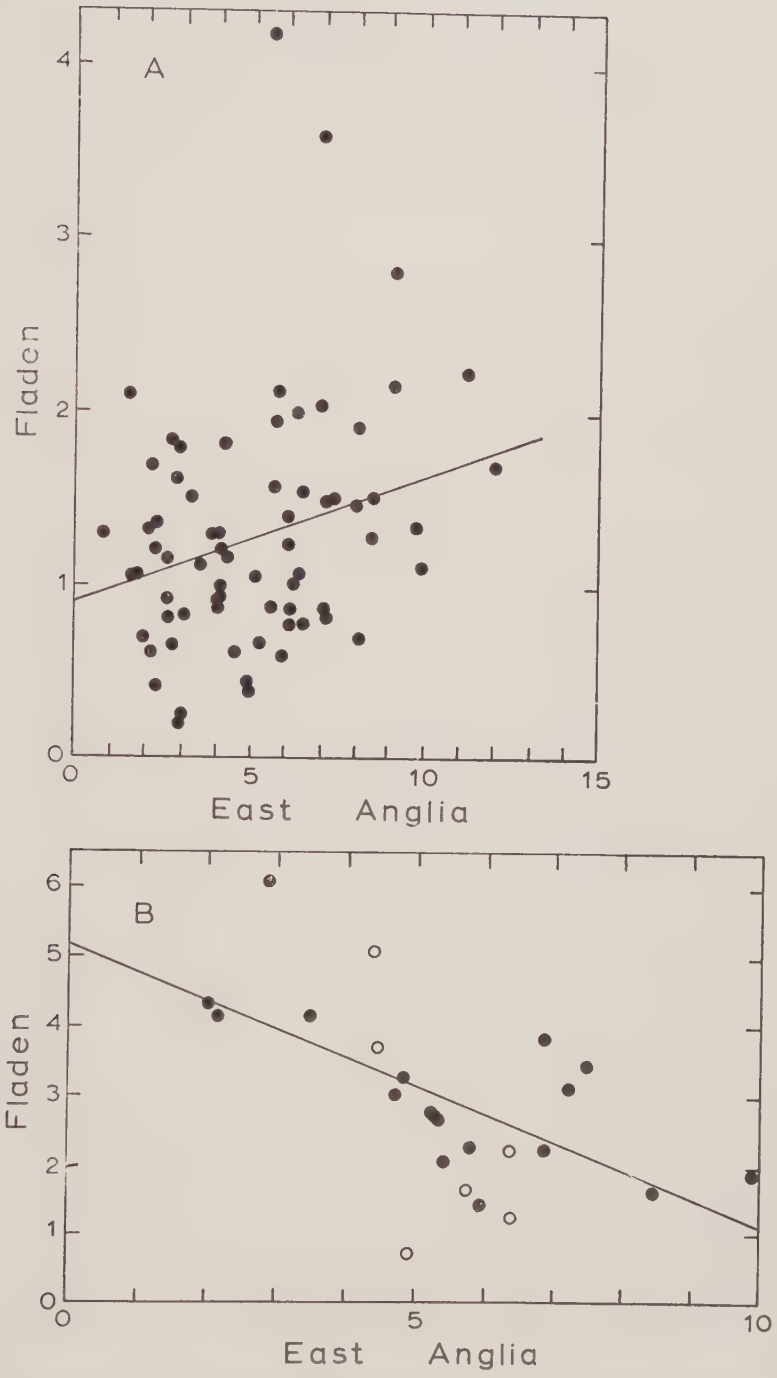

Fig. 19. A. *Regression of stock densities, corrected for mortality and abundance, of all ages on the Fladen and the same at East Anglia, in the period* 1930–50 (1930–2, 1934–6, 1947–50)*; the regression is significantly different from zero.*
B. *Regression of stock densities, corrected for mortality and abundance, of ages* 3 (◯) *and* 4–6 (●) *on the Fladen and the same at East Anglia in the period* 1953–8*; this negative regression is significantly different from zero.*

The relationship between the East Anglian stock and the Buchan pre-spawning stock is given in Figure 20. Figure 20A shows the correlation in the combined data for the ages 4–7 from the years 1930–55 ($r = 0{\cdot}66^{**}$); Figure 20B gives the correlation for the ages 5–7 for the period 1930–8 ($r = 0{\cdot}72^{**}$) and that for the same ages in the period 1952–60 ($r = 0{\cdot}63^{**}$). It should be noted that

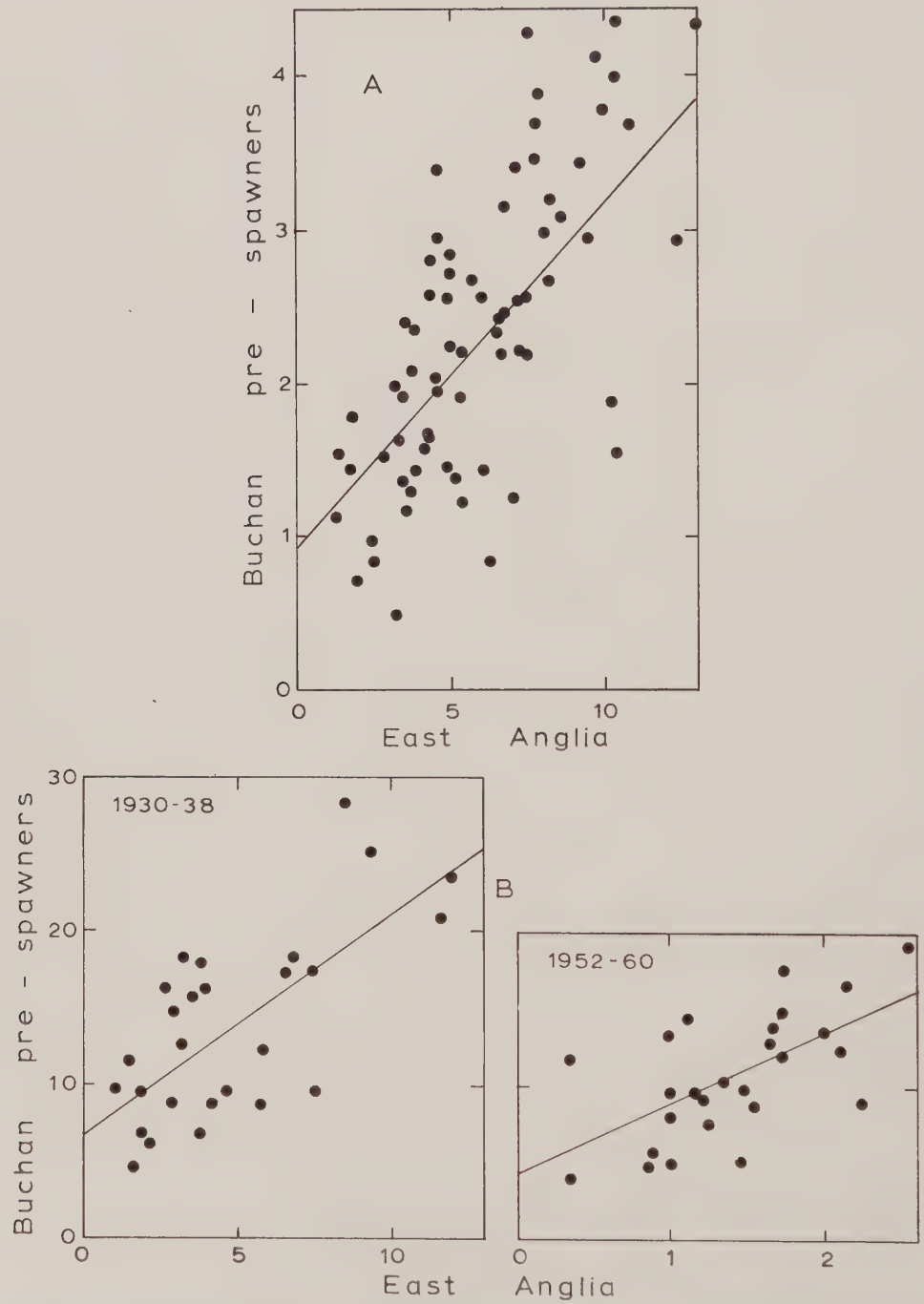

Fig. 20. *Regression of stock densities, corrected for mortality and abundance, in the Buchan pre-spawning fishery, and the same at East Anglia.* A. *Ages four to seven, in the period* 1930–55; *the regression is significantly different from zero.* B. *Ages five to seven, in two periods,* 1930–8 *and* 1952–60; *both regressions are significantly different from zero.*

there is no bias in the combined data due to the recruitment change. This is because the age distributions in East Anglia and in the Buchan pre-spawning fishery were of the same shape before and after the recruitment change. From these results we would conclude that East Anglian fish, particularly the middle-aged ones, were present in the Buchan pre-spawning fishery.

Summarizing the East Anglian results, it appears that there is no evidence of East Anglian fish being present in the Buchan spawning or Shetland fisheries. There is considerable evidence that they were to be found in the Buchan pre-spawning fishery both before and after the recruitment change. On the Fladen ground, there is some evidence that East Anglian fish were present before 1950–2; after that date the technique fails because of the negative correlation, which is probably a year-class effect. The estimates of $(1 - a'/\bar{x})100$ for the mixture of East Anglian stock in the three northern fisheries are:

Buchan pre-spawning fishery

	1930–50	1952–60
ages 3–4		Not significant
ages 5–7		61% ($r = 0{\cdot}63^{**}$)

	1930–55
ages 4–7	59% ($r = 0{\cdot}66^{**}$)

Fladen

	1930–50	1953–8
ages 3–9	30% ($r = 0{\cdot}27^{*}$)	Negative correlation ($r = 0{\cdot}26^{*}$)

(iv) *The mixing of Downs and Dogger spawners in the Dogger fishery*

It may appear a little novel to treat the Dogger fishery as a mixed one. Immature fish are found on the Dogger, as well as fish in maturity stages III and IV (Schubert 1957, 1958, 1959, 1960). It is likely that Downs fish must pass over the wide area which has been described as the Dogger fishery, which ranges from the Northeast Bank and the Northwest Rough to the Silver Pit. Within this extensive area are found a number of spawning grounds, but also a number of grounds, such as Bayman's Hole or Bruce's Garden, which are not spawning grounds. Figure 21 shows the grounds referred to. The Dogger fishery differs from the fisheries in the northern North Sea in that it is unlikely that the Buchan spawners are to be found there in any quantity. Buchan spawners do find their way to the Skagerrak, for Andersson (1950) showed a marked correlation in year-classes between those fish caught in the Skagerrak in late winter and those caught on the Fladen, the very old fish were characteristic of the Buchan spawners. There is no evidence yet that the Buchan spawners are to be found in the Dogger fishery. The relationship between the East Anglian fishery and the Dogger fishery is given in Figure 22 which shows the correlation in the combined data ($r = 0{\cdot}36^{*}$); $(1 - a'/\bar{x})100$ is 36%. No year-class correlation between the Downs and Dogger spawning groups was observed during the fifties (Figure 11) and there are no data for the estimation of year-class correlation between the two groups during the thirties.

During the fifties the same technique breaks down because of the bias referred to earlier, i.e. the individual age series of stock densities corrected for differences in mortality and abundance change significantly with time. The problem has been approached in another way. The Belgian October Dogger fishery has been treated as the spawning fishery and the German Dogger fishery as a mixed fishery (see Section 4). Figure 23 shows the correlation in the combined data ($r = 0{\cdot}43^{**}$); the estimate of mixing, $(1 - a'/\bar{x})100$, is 41%. This result means that less than half of the German Dogger stock is composed of Belgian October Dogger spawners. Therefore it must be composed of Downs spawners

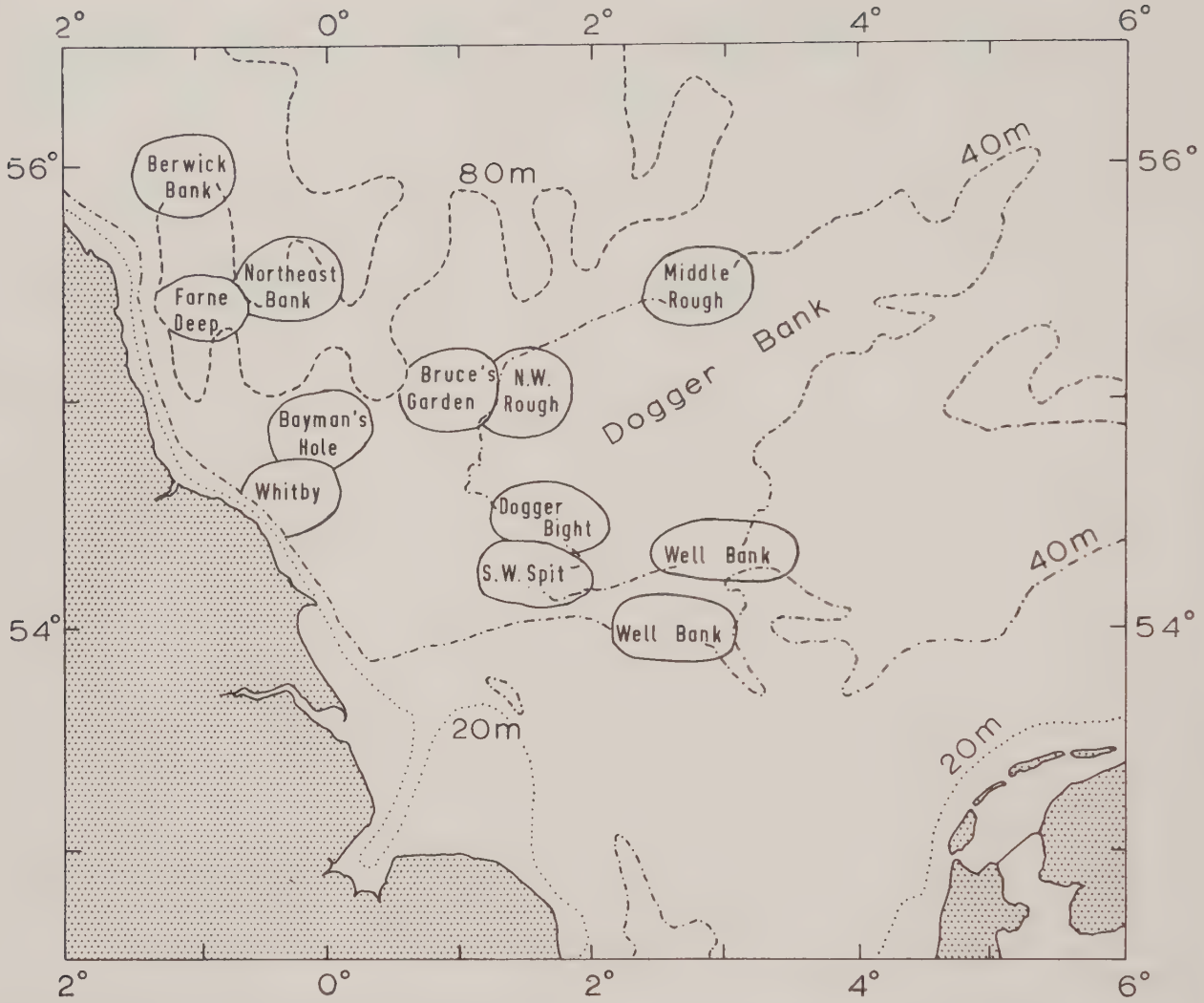

Fig. 21. *Herring grounds worked in the central North Sea, which may be designated as 'Dogger grounds', but not all of which are necessarily spawning grounds.*

and of other spawners, such as the Whitby group, Northeast Bank group, etc. The estimates of mixing were examined by ages; only the individual regressions for the ages 7, 8 and 9 were significant. The trend of $(1 - a'/\bar{x})100$ with age is:

Age:	3	4	5	6	7	8	9
$(1 - a'/\bar{x})100$	23%	17%	45%	19%	66%	101%**	87%
Means	26%				85%		

Such a result implies that the older fish, the seven-, eight-, and nine-year-olds, are common to the Belgian Dogger fishery and to the German Dogger fishery, but that the young fish (3- to 6-year-olds) comprise another component. The age range from three to six is that of the Downs stock during the period and not that of another Dogger component. This also suggests that the Belgian October Dogger stock is a fair sample of the whole Dogger spawning stock.

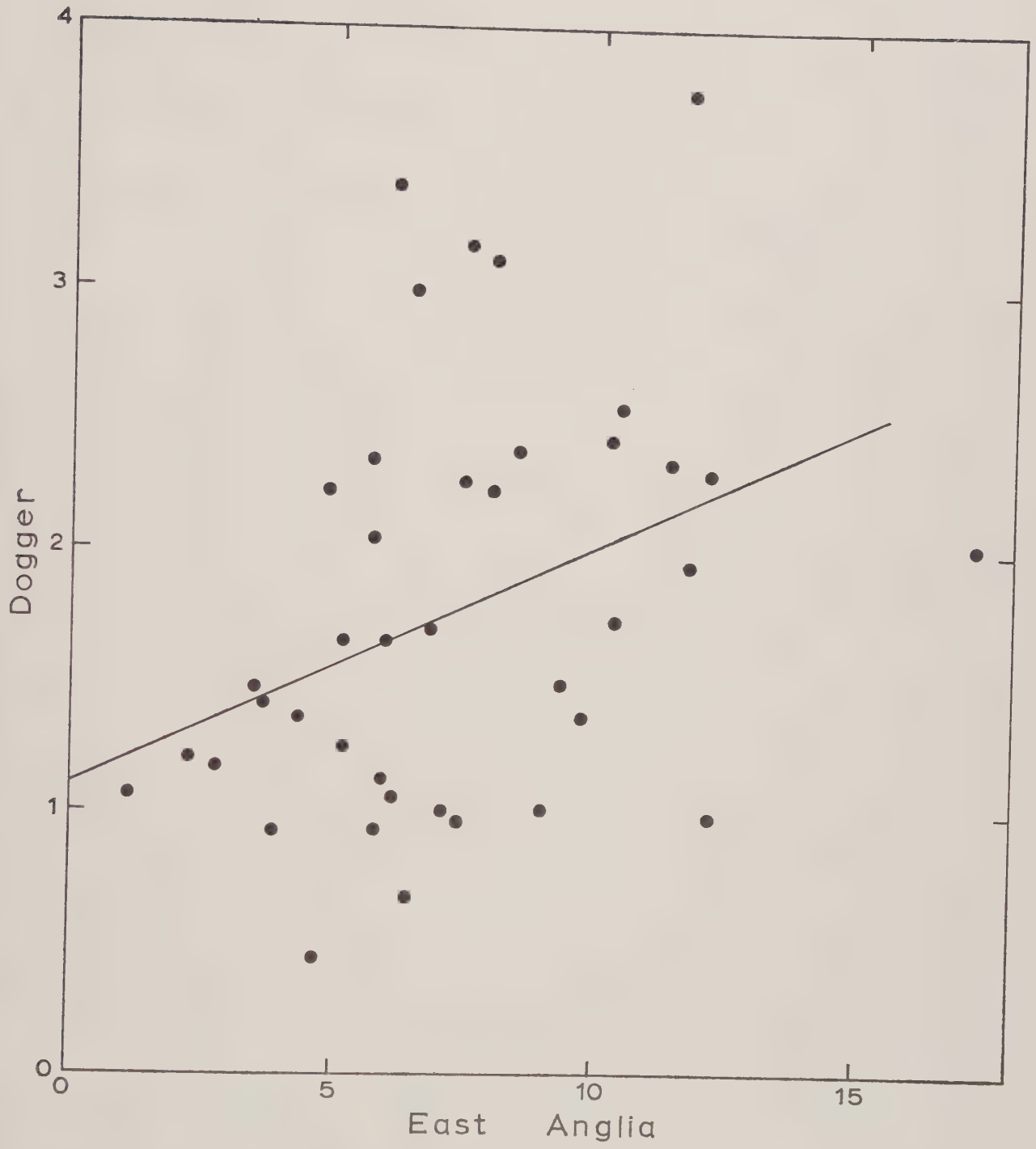

Fig. 22. *Regression of stock densities, corrected for mortality and abundance, on the Dogger, of ages three to six, on the same at East Anglia for the period* 1930–50*; the regression is significantly different from zero.*

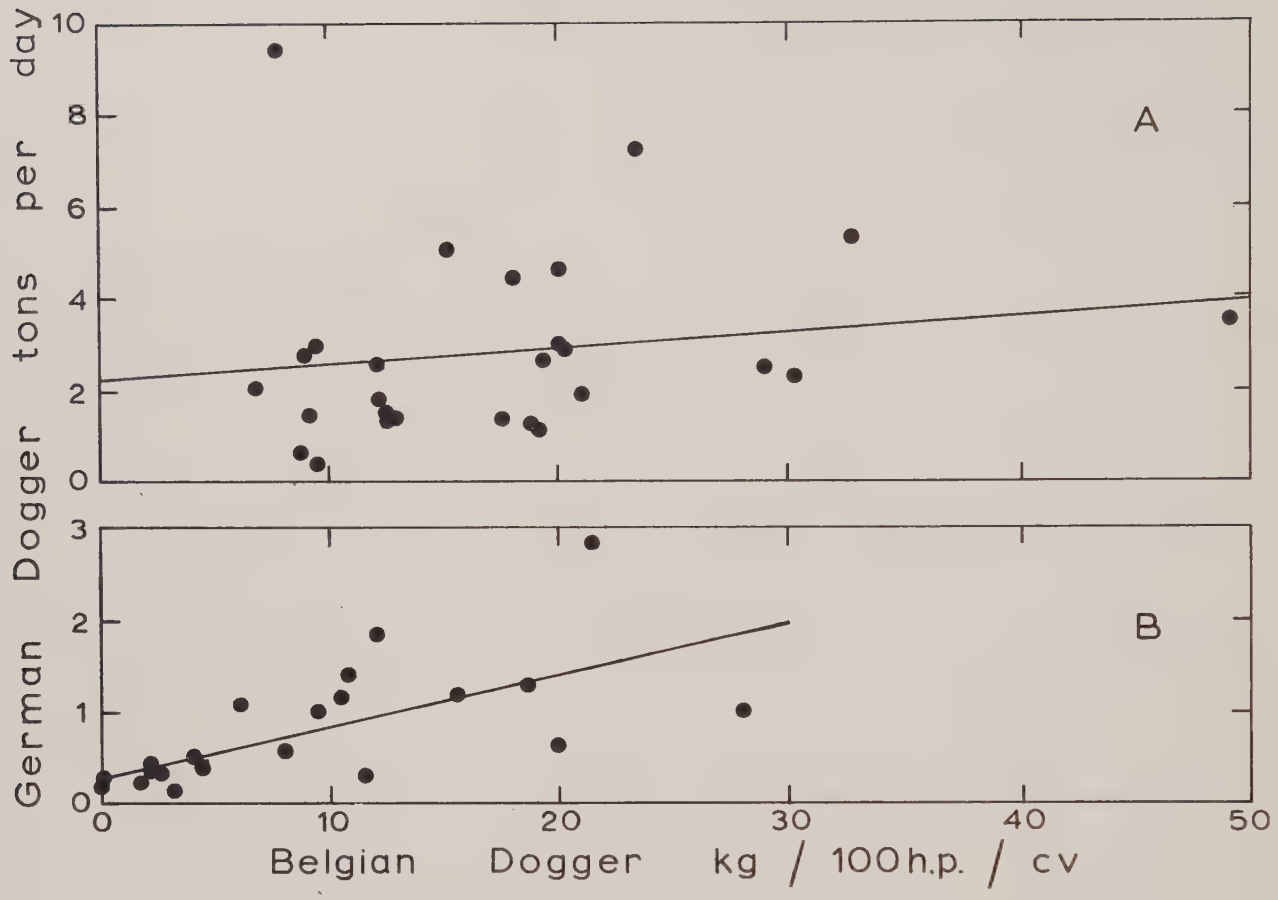

Fig. 23. *Regression of densities of German Dogger stock on Belgian October Dogger stock,* 1949–58 (*excluding* 1951, 1952 *and* 1956). A: *ages three to six;* B: *ages seven to nine.*

It will be shown in the next section that on the Fladen a sharp increase in catch/effort took place in 1951–4, which was independent of changes in recruitment, so far as can be seen. An analysis of the maturity-stage material on the Fladen will suggest that Downs fish were present there in fair quantity during that period. Schubert (1961) shows that a similar increase in catch/effort was observed on the Dogger from 1951–4. It is likely that this increase also was independent of changes in recruitment to the spawning stocks; the dominant year-class during the period 1946–54 was that of 1946, which reached its peak in 1949 (Figure 9). Hence the increase in catch per effort from 1951–4 might have been due to mixers from elsewhere, perhaps Downs fish. Indeed, it is likely that the increase in apparent recruitment to the Fladen, referred to in Section 3, was an increase in mixture of Downs fish, as they grew bigger for their age.

There are three pieces of evidence that can now be linked. The use of the measure $(1 - a'/\bar{x})100$ implies that the greatest pre-war mixing rate of the Downs fish on the Dogger was of the order of one third; after 1950, the remainder from the Belgian/German Dogger mixing proportion was more than a half. It is possible that the proportion of the Downs stock mixing in the Dogger fishery increased in the fifties, which may then account for the observed increase in catch/effort on the Dogger in the period 1951–4. The mixing component in the German Dogger stock was that part aged from three to six, which is the main range of age of the Downs stock. The simplest explanation of these facts is that the German Dogger fishery was a mixed fishery, that the mixing component was the Downs

stock and that the proportion of Downs fish in the German Dogger increased from one third to one half (or even two thirds) during the early fifties.

(v) *Summary*

The data shown in Figures 13 to 20 may be summarized by tabulating the estimates of $(1 - a'/\bar{x})100$, with the correlation coefficients. The pre-recruitment change data are given in Table 7 and those after the change are given in Table 8.

Table 7. *Estimates of* $(1 - a'/\bar{x})100$ *from the correlation between catches and effort, for two spawning groups in the three northern fisheries during the thirties and forties*

Mixed fishery	Spawning group			
	Buchan spawning		East Anglia	
	Ages		Ages	
Buchan pre-spawners	3–4 5–7	43% ($r = 0{\cdot}40$*) 40% ($r = 0{\cdot}43$**)	4–7	59% ($r = 0{\cdot}66$**)
Shetland	3–9	28% ($r = 0{\cdot}30$*)		—
Fladen		—	3–9	30% ($r = 0{\cdot}27$*)

NOTE: There are no data available on the Dogger spawning fishery before 1949.
* Correlation coefficient significant at $p = 0{\cdot}05$.
** Correlation coefficient significant at $p = 0{\cdot}01$.

Table 8. *Estimates of* $(1 - a'/\bar{x})100$ *from the correlation between catches and effort, for three spawning groups in the three northern fisheries during the fifties*

Mixed fishery	Spawning group					
	Buchan spawning		East Anglia		Dogger spawning	
	Ages		Ages		Ages	
Buchan pre-spawners	3–4 5–7	79% ($r = 0{\cdot}67$**) 40% ($r = 0{\cdot}40$*)	5–7	— 61% ($r = 0{\cdot}63$**)	3–4 5–8	65% ($r = 0{\cdot}64$**) 54% ($r = 0{\cdot}56$**)
Shetland	3–9	79% ($r = 0{\cdot}77$**)		—	5–9	24% ($r = 0{\cdot}35$*)
Fladen	3–5	74% ($r = 0{\cdot}69$**)	5–9	Negative ($r = 0{\cdot}26$*)	3–8	59% ($r = 0{\cdot}59$**)

NOTE: * Correlation coefficient significant at $p = 0{\cdot}05$.
** Correlation coefficient significant at $p = 0{\cdot}01$.

The estimates of $(1 - a'/\bar{x})100$ for the Buchan pre-spawning fishery, ages 5–7 (or 5–8), during the fifties add up to 155%. This does not happen in other estimates. It is possibly due to the fact that the older East Anglian fish were abundant during the period 1951–4 and that older Buchan spawning

fish were abundant from 1955–9. This effect has been shown to occur on the Fladen (see the next section, on the analysis of maturity-stage data).

Table 9 summarizes the results obtained from the analysis of Dogger data:

Table 9. *Estimates of* $(1 - a'/\bar{x})100$ *from the correlation between catches and effort in East Anglia and in the October Belgian Dogger fishery (treated as spawning fisheries) on those of the German Dogger fishery (treated as a mixed fishery)*

	1930–50	1949–58
East Anglia on Dogger, ages 3–6	36% ($r = 0{\cdot}36$*)	—
Belgian Dogger on German Dogger, ages 3–9	—	41% ($r = 0{\cdot}43$*)

* Correlation coefficient significant at $p = 0{\cdot}05$.

Comparing Tables 7 and 8 it will be seen that the East Anglian component in the Buchan pre-spawning fishery (ages 4–7) was about the same before 1950 as it was after that date. The Buchan spawning component of recruits increased in the Buchan pre-spawning fishery after the recruitment change, but the proportion of older Buchan spawners has remained constant there through the recruitment change. On the Fladen before the recruitment change there must have been very few Buchan spawning recruits indeed and not many older fish; after the recruitment change, the proportion of Buchan spawning recruits on the Fladen increased greatly, but the proportion of older fish did not increase so much. At Shetland before the recruitment change there was a small proportion of Buchan spawners, but after it the Shetland fishery consisted in the main of Buchan spawners of all ages. After the recruitment change, there was a small proportion of Dogger spawners in the Shetland fishery. There are no pre-war samples of Dogger spawners, but in the Shetland material for that period there is an unspecified remainder, which might have been composed either of Dogger spawners or of spring spawners.

From Table 9 it would appear that because the Belgian Dogger spawners only account for about one third of the general Dogger fishery, part of the remainder could well be Downs spawners; indeed the pre-war mixing rate suggests that one third were Downs spawners. It is possible that the proportion of Downs spawners increased during the later period.

EVIDENCE OF THE MIXING OF DOWNS HERRING IN THE NORTHERN NORTH SEA FROM THE DISTRIBUTIONS OF MATURITY STAGES

INTRODUCTION

Wood's (1930) table (Table 3 in this paper) showed that fish on the Fladen ground and those on the Scottish north-east coast could be distinguished by their degree of maturation; the justification for the separation is shown by differences in length for age in the separated groups.

On the Fladen ground after 1950 a sharp increase in the proportion of fish in maturity stage V was found. An attempt was made to analyse the data by maturity stages. To some extent it will be shown that this method gives an estimate of mixing which is quite independent of that derived in the previous section.

METHOD

The method is simple: to estimate the relation between the stock densities of given maturity stages in the mixed fisheries and those of 'pure' stocks, Downs, Dogger spawning or Buchan spawning groups; i.e. $y = a + bx$,

where y is the stock density of (for example) maturity stage V in the mixed fishery;

where x is the stock density of maturity stage V in a pure (or spawning) stock;

where b represents the dependence of stock density, in (for example) maturity stage V in the mixed fishery, on that in the pure fishery;

where a represents that part of the stock in maturity stage V in the mixed fishery which is not part of the pure stock.

If the pure stock is estimated for one age group, then the intercept represents fish in stage V of that age in other stocks and fish in stage V of other ages, but of any stock. Hence the use of slope and intercept separates the pure stock in the one age group from other stocks. Fish change from maturity stage to maturity stage fairly quickly and so the stock densities in the mixed fishery are always taken from the same month, as, for example, August on the Fladen.

One most important point is the nature of the correlation when found. The correlation is of the same nature as that used in the previous section except that there can be no year-class correlation. Bias is not generated by differences in age with time or by differences in abundance with age. Correlation is probably generated by mixture only and so a better measure of mixing is found. The estimate of mixing is given by $(1 - a/\bar{y})100$, representing that part of the single stock found in the mixed fishery.

RESULTS

Figure 24 shows the analysis of maturity stages on the Fladen ground. Regressions of all three stocks (Dogger, Buchan and East Anglia) have been investigated on all maturity stages; only those for maturity stages IV and V, with one exception, yielded clear results. The age groups have been separated as 'recruiting fish' (four-year-old fish before 1951 and three-year-old fish after that date) and 'middle-aged' fish (five-, six- and seven-year-old fish). The data have been split into two periods, 1932–54 and 1955–9. The reason for this is that the Buchan spawners have increased in abundance since 1953; therefore the increase in older fish (5, 6 and 7) could not appear before 1955. The increase in the Buchan stock has amounted to about three times, and we would expect some of these fish to be in maturity stages IV and V in the northern North Sea. The estimates of $(1 - a/\bar{y})100$, with correlation coefficients, are set out in Table 10.

Of the recruits the East Anglian fish were correlated markedly with the Fladen stock in maturity stage V from 1932 to 1954; from 1955 to 1959 the recruit Buchan spawners were also correlated with the Fladen stock. The Fladen stock in maturity stage IV was correlated with the middle-aged East Anglian stock from 1932 to 1954, and with the middle-aged October Dogger stock from 1949 to 1954; from 1955 to 1959 the middle-aged Buchan spawners were correlated with the same stock. Thus it would appear that until the threefold increase in the Buchan stock by 1955, the Fladen fishery was composed of East Anglian recruits and of middle-aged fish of both the East Anglian stock and the October Dogger stock. From 1955 to 1959, Buchan spawning recruits and October Dogger middle-aged fish were present. For the whole period, 1932–59, average values of recruit East Anglian stock and Buchan spawning stock can be derived. From 1955–9, the middle-aged East Anglian stock had been reduced to very low levels and so no correlation should be expected with the Fladen stock, so

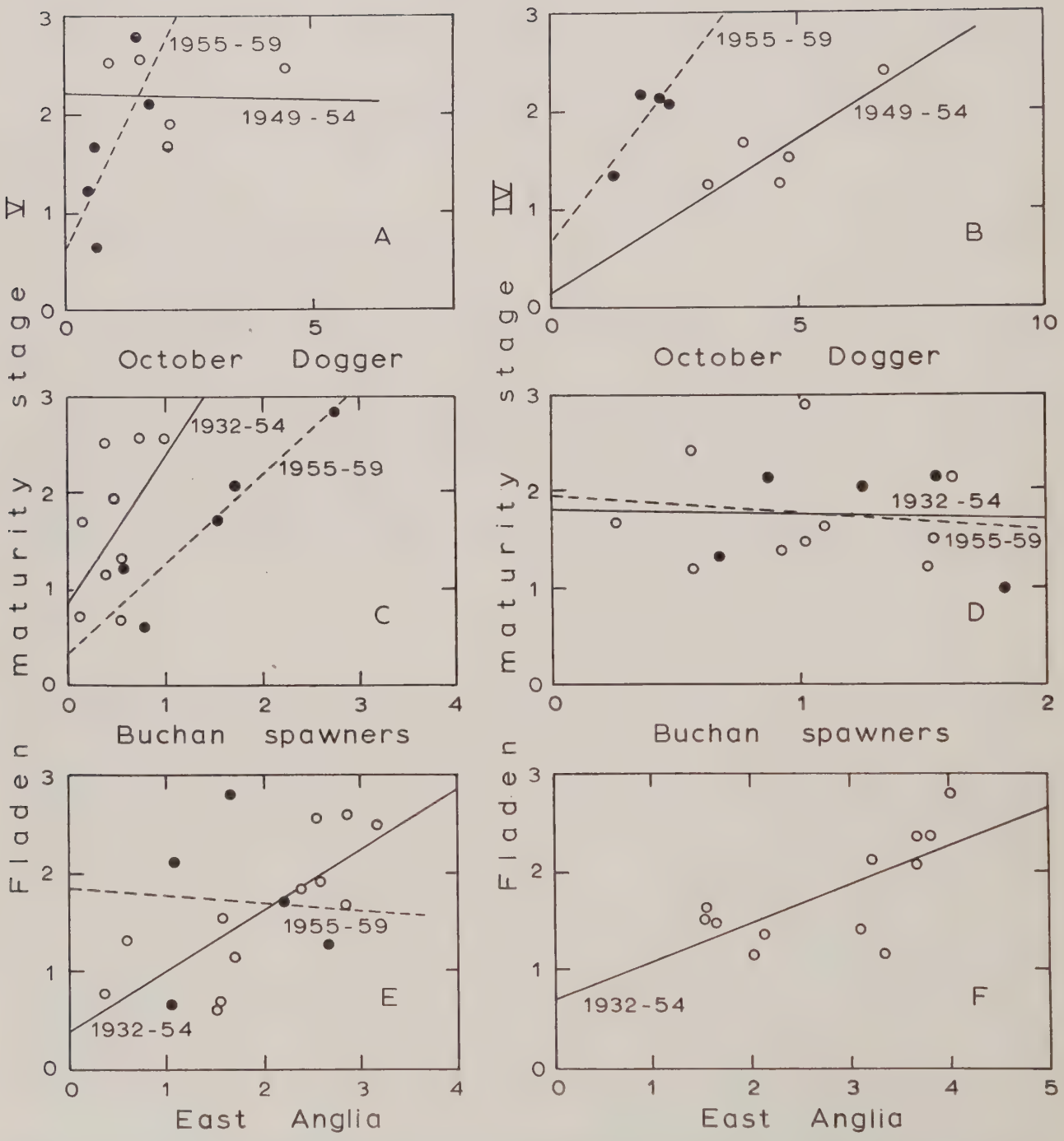

Fig. 24. *Regressions of stock densities, as maturity stages on the Fladen, on stock densities of recruit or middle-aged spawners:* A. *Fladen stage V on October Dogger recruits* (3- *or* 4-*year-olds*); B. *Fladen stage IV on October Dogger middle-aged fish* (5-, 6-, 7-*year-olds*); C. *Fladen stage V on Buchan spawner recruits;* D. *Fladen stage IV on Buchan spawner middle-aged fish;* E. *Fladen stage V on East Anglian recruits;* F. *Fladen stage IV on East Anglian middle-aged fish.*

Table 10. *Estimates of mixing* $(1 - a/\bar{y})100$ *for three periods, from the analysis of stock densities in maturity stages IV and V on the Fladen*

	1932–54		1955–9		1932–59	
	$(1 - a/\bar{y})100$	r	$(1 - a/\bar{y})100$	r	$(1 - a/\bar{y})100$	r
Recruit East Anglians on stage V	75%	0·79 (0·01)	—	—	57%	0·56 (0·02)
Recruit Buchan spawners on stage V	—	—	79%	0·93 (0·01)	29%	0·52 (0·05)
	1949–54		1955–9		1949–59	
	$(1 - a/\bar{y})100$	r	$(1 - a/\bar{y})100$	r	$(1 - a/\bar{y})100$	r
Recruit October Dogger spawners on stage V	—	—	—	—	—	—
	1932–54		1955–9		1932–59	
	$(1 - a/\bar{y})100$	r	$(1 - a/\bar{y})100$	r	$(1 - a/\bar{y})100$	r
East Anglian middle-aged stock on stage IV	63%	0·70	—	—	—	—
Buchan spawning middle-aged stock on stage IV	—	—	—	—	—	—
	1949–54		1955–9		1949–59	
October Dogger middle-aged stock	90%	0·86 (0·05)	67%	0·82 (0·05)	—	—

NOTE: The blanks in the table mean that the correlation coefficients were not significantly different from zero; in such cases $(1 - a/\bar{y})100$ was not estimated.

long as other components were present. Perhaps the same is true of the East Anglian recruits. A significant correlation emerges in the period 1932–59, but not in 1955–9, perhaps because it is masked by the strong Buchan 1956 year-class.

Figure 25A shows the time series of the percentage in maturity stage V on the Fladen ground from 1932 to 1959; Figure 25B shows that of the percentage in maturity stage IV for the same period. The high values for stage V were reached in 1950, and from 1950 to 1954 the average quantity was much higher than that found in the preceding years, 1932–49. The average quantity is a little lower from 1955 to 1958; in 1959 (and 1960) the large 1956 year-class came in. The same sequence of events is not shown in the distribution of stage IV fish, presumably because the recruitment changes, of 1950–2, would affect the stocks of middle-aged fish only slightly. It is noteworthy that the increase in the Buchan stock in the middle fifties is not manifest in the time series of stage IV – which supports the conclusion already reached from the regressions given in Section 4 that the older Buchan stock does not reach the Fladen fishery. The sharp increase on the Fladen of stock in maturity stage V took place before the stock increase to the Buchan spawning fishery; hence the increase must have been of East Anglian or Dogger fish. This may well have been associated with the early increase in apparent recruitment to the Fladen fishery long before the increase in abundance of Buchan spawners in 1953, as noticed in an earlier section.

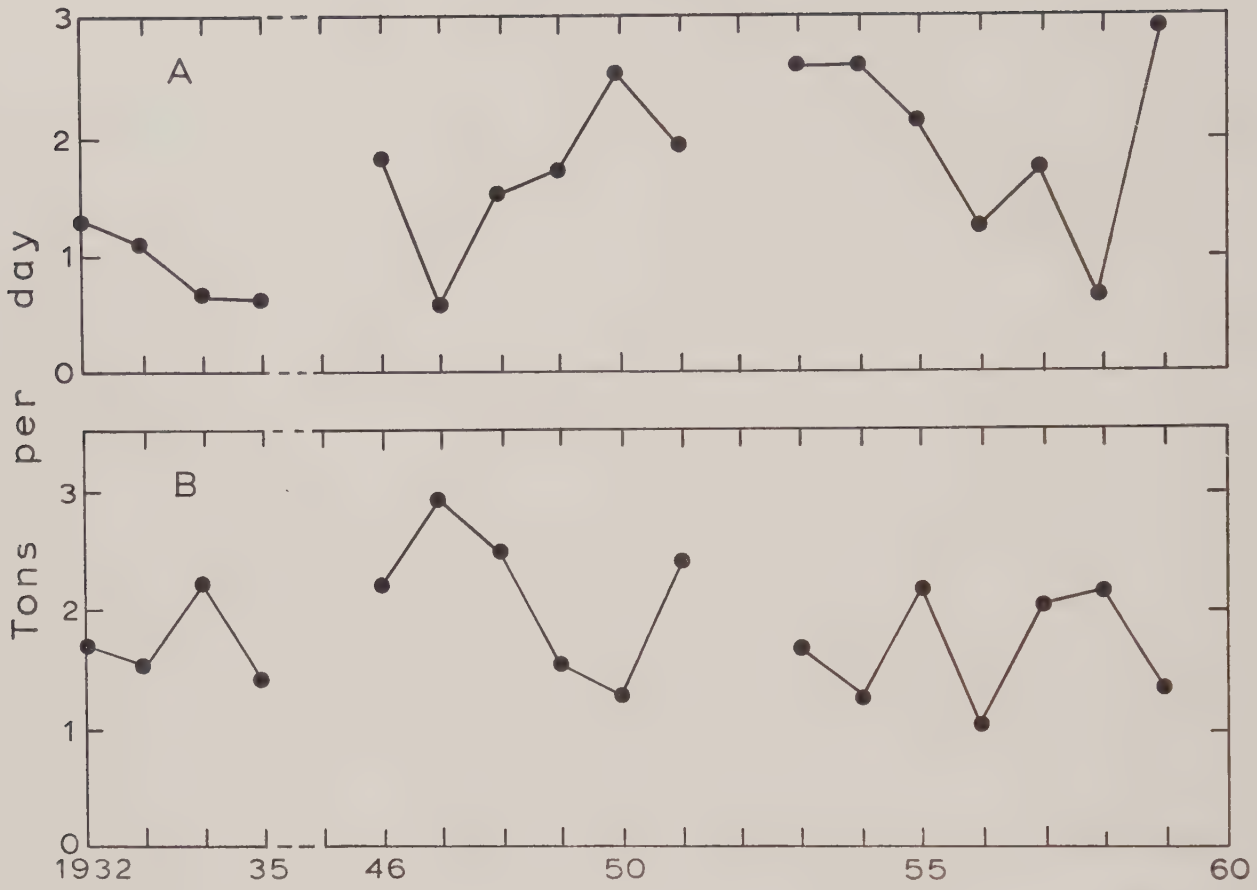

Fig. 25. *Time series of stock densities on the Fladen from* 1932–59; A. *in maturity stage V*; B. *in maturity stage IV*.

The three-year-old fish in 1950 in East Anglia were much bigger than their predecessors; this was perhaps associated with the increased abundance of *Calanus* in that year. Indeed the increase in mean length in that year was the largest in the time series of mean lengths from 1920 to 1958. The fish in maturity stage IV increased in proportion on the Fladen in 1951. In East Anglia, the fish older than three showed the biggest increments in length (3/4, 4/5, 5/6) between 1950 and 1951. In Schubert's paper (1961) a sharp increase in catch/effort on the Fladen is recorded for 1951, as compared with a steady decline in the immediately post-war years shown in Figure 25A. Perhaps the proportion of all Downs fish increased in 1951 on the Fladen, as they became bigger for their age. The best year-class of all Dogger and Buchan classes at this time was the 1946 year-class, which should have reached its peak in 1950 at four years of age. Figures 9 and 10 show the recruitments to the Dogger spawning and Buchan spawning fisheries as well as the apparent recruitment to the Fladen and Dogger fishery. It will be seen that the 1946 year-class, dominant in the Dogger spawning stock, was not noticeable in the Dogger fishery. This must mean that the added stock in 1951–4 on the Dogger was Downs fish. The questions are whether the sharp increase in length of three-year-olds in 1950 in Downs fish caused the increase in fish at stage V in 1950 on the Fladen, and whether the larger increments put on by older fish by 1951 in Downs fish were associated with the increased catch/effort in that year on the Fladen.

Taking the observations in the series in time order, Figure 25A shows a peak of stock in maturity stage V in 1950 and Figure 25B shows one of stock in maturity stage IV in 1951. The simple association in time of two events in length of fish in the East Anglian fishery with two events in catch per effort

on the Fladen ground is not convincing. But as the East Anglian stock is linked with the Fladen stock by maturity stages as in Figure 24, the association is confirmed. A most interesting point is that the correlations of East Anglian stock with the stocks of the two maturity stages appear to be associated with the increases in length in the East Anglian fishery. In other words, as the fish grew bigger for their age, a larger proportion of fish in the maturity stages IV and V was found on the Fladen. Parrish and Craig (1964) have shown that the biggest fish of an age group tend to be found further north during the summer fishery. Hence, as the fish became bigger in the early fifties, they would be expected to move further north in the summer fishery.

The regressions in Figure 24 may well mean that East Anglian fish are on the Fladen in maturity stages IV and V. Then the recruiting East Anglian fish are in maturity stage V when the middle-aged fish are in maturity stage IV. Also, the recruiting East Anglian fish are in maturity stage V in August. Neither possibility conflicts with Iles' (1964) concept of a long stage V for winter spawners, nor with the well-known age sequence in East Anglia of recruit fish in October and older fish in November (Hodgson, 1939). An apparent conflict does arise in Burd's (Burd and Cushing, 1962) evidence that East Anglian recruits are below stage IV at Shields in July; similar work has suggested that the East Anglian fish at Shields are *below* stage V in August (Burd: personal communication). This conflict can be resolved by supposing that the larger fish of a year-class migrate further north in summer and mature earlier. This supposition would make sense of an East Anglian phenomenon so far unexplained– that within a year-class, the larger fish enter the fishery first and the smaller ones last. The prime question which forms the keystone to this little complex of problems is whether the bigger fish of a year-class are in a later maturity stage at a particular time. Mr. Burd has allowed me to use the following table of mean lengths at different maturity stages at North Shields in June, July and August, 1960, for the ages three and four.

Table 11. *Mean lengths (cm) at different maturity stages in June, July and August* 1960 *for fish aged three and four at North Shields*

	3			4		
	June	July	August	June	July	August
III	23·75	23·84	23·65	24·66	24·80	25·01
III–IV	24·37	24·29	23·82	24·78	25·05	25·29
IV	24·11	24·10	24·34	25·11	25·13	25·43
IV–V		24·45	24·45		25·41	25·81
V		24·60	24·65	25·30	25·70	25·84
VI		24·55			25·72	

NOTE: In July and August, the upper parts of the divided column probably represent Downs fish and the lower parts probably represent fish of the Bank stock.

The table shows that the larger fish are in the more advanced maturity stages. Parrish and Craig (1964) show that the bigger fish of an age group tend to live farther north. So we might expect that the farther north the fish, the more advanced their stage of maturation.

Figure 26 shows the results of maturity-stage analysis as applied to the Scottish fisheries in July. Highly significant correlations exist between the Buchan middle-aged spawners and the virgin Buchan pre-spawning stock in May and June. Mr. Parrish has told me that the proportion of fish in maturity stage I from 1957 to 1960 amongst the fish of five to seven years of age does not exceed 8%. Hence

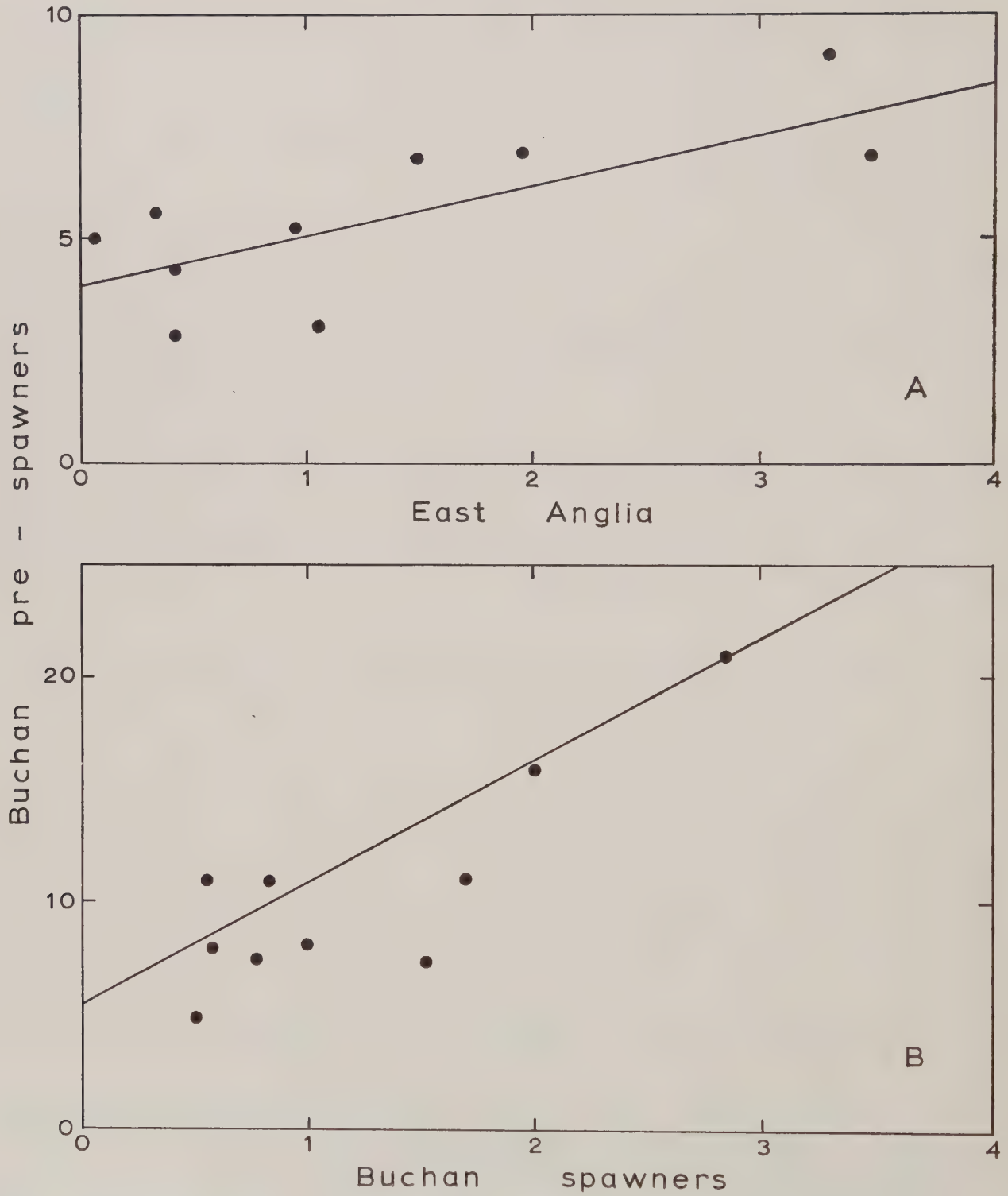

Fig. 26. *Regression of stock densities, as maturity stages (in the Buchan pre-spawning fishery), on stock densities of spawning fish,* 1951–60.

A. *Buchan pre-spawners in stage II in July on middle-aged East Anglian fish;* (5-, 6- and 7-*year-olds*).

B. *Buchan pre-spawners in stage III and IV in July on recruit Buchan spawners;* (3- *and* 4-*year-olds*).

the regression is possibly spurious. When the data are plotted as a time series (not illustrated) the spuriousness is revealed. The stock densities of the virgin fish build up to a peak in 1955, after which they decline; the same is true for the middle-aged fish and this cannot be for reasons of abundance changes.

Let us consider the other regressions emerging from this analysis. There is a significant correlation between the middle-aged Buchan spawners and the abundances of stage III in June. There is also a significant correlation between the recruit Buchan spawners and the abundance of stages III and IV in July (Figure 26B), and between stages I, II, III and IV in the Shetland fishery and the recruit Buchan spawners (not illustrated). Each correlation found is that which might have been expected from the technique used in the previous section. The Shetland correlation was limited to recruit Buchan spawners; in the Buchan pre-spawning fishery, half were said to be Buchan spawning recruits and a small proportion were said to be middle-aged Buchan spawners; a correlation was found between middle-aged East Anglian fish and the Buchan pre-spawning fishery. It is interesting that the maturity analysis shows a correlation between middle-aged East Anglian fish and the abundances of maturity stage II in July (Figure 26A). Table 12 summarizes the estimates of mixing rates.

Table 12. *Estimates of mixing* $[(1 - a/\bar{y})100]$ *for the period* 1951–60, *from the analysis of stock densities in some maturity stages in the Buchan pre-spawning fishery*

'Pure stocks'	Stage III (June)		Stages III, IV (July)		Stage II (July)	
	$(1 - a/\bar{y})100$	r	$(1 - a/\bar{y})100$	r	$(1 - a/\bar{y})100$	r
East Anglia (ages 3–7)	—		—		28%	
Buchan spawners (ages 3, 4)	98%		51%		—	

The estimates of mixing from the analysis of maturity stages on the Fladen and in the Scottish fisheries are quite independent of those calculated from stock densities alone as in the previous section. Yet the results are of the same order. The percentages in maturity stages IV and V on the Fladen from 1932–49 were 30% and 19% respectively. From Table 10, 75% of the fish in stage V were East Anglians and 63% of those in stage IV. The total quantity of East Anglian fish before the recruitment change is given by $(75\% \times 19\%) + (63\% \times 30\%) = 33\%$. The estimate using the stock correlation method is 30%. Such comparisons cannot be made in all the material; but the Buchan spawners were found to be absent on the Fladen in the earlier period with both techniques, and the October Dogger spawners were shown to be present in the later period.

There is thus some degree of independent confirmation of the estimates of mixing calculated by the method of stock correlation. There is consistency within the results. The main biological difficulty is that recruit fish appear to be in maturity stage V when the older fish are still in maturity stage IV. This might be reasonable for the East Anglian stock, where the younger fish appear in October and the older fish in November. For the other two stocks there is no evidence that this sequence exists in spawning, nor that recruits are in stage V when middle-aged fish are in stage IV.

THE MIXING OF THE THREE SPAWNING GROUPS IN THE MIXED FISHERIES

Tables 7, 8 and 9 give estimates of $(1 - a'/\bar{x})100$ from the method of stock correlation. Table 10 gives estimates of $(1 - a/\bar{y})100$ from the method of maturity-stage analysis. Some values in all tables are for selected age groups and hence overestimate the proportion of a stock in a mixed fishery.

For example, if only the three-year-old fish of a single stock were contributing to the mixture, then the proportion in the mixed fishery must be multiplied by the percentage of three-year-olds in the single stock. Table 13 gives the proportions of the single stocks in the mixed fisheries based on the method of stock correlation, from Tables 7, 8 and 9.

Table 13. *Proportions of the three spawning groups in the mixed fisheries, from the method of stock correlation*

A. Three northern fisheries, before 1950 (*using data from Table* 7)

	Buchan spawners	East Anglia
Buchan pre-spawners	40%	44%
Shetland	28%	—
Fladen	—	30%

B. Three northern fisheries, after 1950 (*using data from Table* 8)

	Buchan spawners	East Anglia	Dogger spawners
Buchan pre-spawners	53%	5%	50%
Shetland	72%	—	12%
Fladen	49%	—	48%

C. The general Dogger fishery (*using data from Table* 9)

	1930–50	1949–58
Spawning groups:		
East Anglia	29%	—
October Dogger	—	41%

Table 14 gives the proportions of the single stocks in the Fladen, based on the method of maturity-stage analysis, using data from Table 10.

Table 14. *Proportions of the three spawning groups on the Fladen, from the analysis of maturity stages*

		1932–54	1955–9	1932–59
East Anglia	Recruits	24%	—	22%
	Middle-aged	26%	—	—
		50%	—	22%
Buchan spawners	Recruits	—	48%	13%
	Middle-aged	—	—	—
			48%	13%
October Dogger	Recruits	—		—
	Middle-aged	37%	28%	—
		37%	28%	

Because it is possible that the proportions on the Fladen changed after 1954, the decade 1951–60 has been split in two parts. The percentages in maturity stages IV and V on the Fladen in the two periods were:

	IV	V
1950–4	29	42
1955–60	35	32

The proportions of the three spawning groups for these two periods are given in Table 15.

Table 15. *Proportions of the three spawning groups on the Fladen during the fifties, from the analysis of maturity stages*

	1950–4	1955–9
East Anglia	50%	19%
Buchan spawners	—	48%
October Dogger	37%	28%

If we compare Table 13B with Table 14, there is an apparent conflict: that during the fifties, by the stock correlation method, there are only Buchan and Dogger spawners on the Fladen, whereas by the maturity-stage analysis East Anglian spawners are present. It will be recalled that there was a sharp negative correlation between East Anglia and Fladen during the fifties, perhaps due to a year-class correlation (see Section 5). Table 15 shows how Buchan spawners replaced East Anglian and Dogger spawners during the late fifties. Hence it is thought that the maturity-stage analysis yields a better picture of the Fladen during the fifties than does the method of stock correlation.

The Dogger is a special and difficult case. From Table 13C, the East Anglian proportion has increased from 29% before 1950 to 59% after 1950. There is no means of knowing how much of the spawning stock is represented by the October fishery, but it is likely that the East Anglian component in the general Dogger fishery increased in the early fifties. A reasonable estimate would suggest that the East Anglian proportion increased from 30% to 50%. In addition to this estimate, the proportions to be used in later sections will be taken from Table 13A, Table 13B (excluding the Fladen) and Table 15. It is thought that these proportions are the best available for the years 1924–60. Each is subject to a fairly large error about the intercept, as shown in the worked example in Section 4.

To summarize: the main natural changes that have taken place to the North Sea herring stocks since the thirties are, firstly, an increase in the length for age, and secondly (and consequentially) changes in the recruitment pattern. The results of the stock analyses show an average condition before 1950, which may have been slowly changing with the gradual increase in length for age taking place at that time. In this average condition, East Anglian fish were found on Fladen and on Dogger (comprising one quarter to one third of the stock) and in the Buchan pre-spawning fishery (comprising about one third or more of the stock). The Buchan spawners were a small group (from Section 2, one sixth of the East Anglian stock in stock density) found in minor proportions in the Buchan pre-spawning fishery and in the Shetland fishery. Of the make-up of the October Dogger stock, there is no direct evidence.

In the period 1950–2, length for age increased in all North Sea herring fisheries. At the same time, the fish recruited earlier in their lives in all three spawning groups and the Buchan spawning stock increased by about three times in the following years. The Buchan spawners were found in greater proportion in the pre-spawning fishery and in Shetland, and their recruits were found for the first time on the Fladen. These changes were an effect of the increased abundance of the Buchan

spawners. Whether the increase in Buchan spawners was an effect of increased total recruitment to North Sea stocks or whether it occurred at the expense of Dogger spawners is unknown (Figure 2).

As a consequence of the increased length for age in the early fifties it is possible that East Anglian fish moved north in greater quantities. It has been shown elsewhere that in summer the bigger fish are found farther to the north. Hence, if the fish grew faster we would expect their summer migration to extend farther northward. It is possible that the East Anglian recruits appeared in numbers on the Fladen in stage V in 1950, when the three-year-old fish were markedly bigger than at any time recorded. Then the older fish appeared on the Fladen in 1951, associated with the biggest growth increments found in the recorded data. Thus it is possible that part of the high catches/effort found on the Fladen and on the Dogger in the period 1951–4 were East Anglian fish. There was no increase in stock in East Anglia in the early fifties (indeed, probably a decrease), but the increase in length for age probably extended the summer migration to the north, making the stock more vulnerable to fishing.

Hence we might expect two relationships to emerge from data collected in the future:

1. Between length for age and size of stock in the Buchan spawners; as length for age increases, so does the size of the stock.
2. Between length for age and the proportion of East Anglian fish on Fladen or Dogger; as length for age increases so more East Anglian fish migrate north in summer.

6. DISCUSSION AND SUMMARY

The Downs stock was defined as the stock of adult autumn-spawning herring that spawns in the Southern Bight of the North Sea and in the Eastern Channel in November and December. Within the fisheries exploiting this stock in the Southern Bight and Eastern Channel, it was shown that the vital parameters of mortality and recruitment were homogeneous. In contrast there were persistent differences in mortality between the Dogger and the East Anglian fishery. Further, there was no correlation in total recruitment between any of the three spawning groups, Buchan spawners, Dogger spawners and Downs spawners. This point confirms the distinctness of the Downs stock from the Dogger and Buchan spawners (sometimes classed as the 'Bank' stock) and suggests that the Dogger and Buchan spawners are each stocks in the sense that the Downs stock is one, i.e. that the adults appear to return to their grounds of first spawning (Burd and Cushing, 1962).

Differences in length for age are found between the three groups of spawners (ICES, 1965) and there are persistent differences in meristic characters (l_1, VS, and K_2). These differences mean that there is a segregation of spawners to the three spawning grounds in the recruitment mechanism, because there is no trend in difference with age and it is as distinct at the age of first recruitment as it is in old age. The segregation in the recruitment mechanism could be a segregation of spawners to their native grounds or it could be a segregation merely in the timing of the recruitment mechanism. The difference in meristic characters between spawners suggests the former (as Zijlstra (1958) pointed out) but the evidence could be equally well interpretable the other way, if there were a trend of meristic character with length. In default of evidence that herring return to their native grounds to spawn, the stock is defined as the adult fish on the spawning ground, to which they return each year after their first spawning.

There is considerable evidence that the Downs fish penetrate the northern and central North Sea during the summer feeding season (Wood, 1930, 1937; Krefft, 1954; Burd and Cushing, 1962). An attempt was made to estimate the proportions of Downs fish in the feeding fisheries. Because there was no year-class correlation between any of the three spawning groups, it was possible to estimate mixture by correlating a mixed stock density with a pure stock density (i.e. that of one of the spawning

groups). In this way it was shown that Downs fish were found in the Buchan pre-spawning fishery, on the Fladen, and in the Dogger fishery; they were absent from the Buchan spawning fishery and the Shetland fishery. For the data from the fifties, the method did not work for the Fladen fishery or the Dogger fishery because of a bias described in the text. However, a second method for use with the Fladen fishery was devised, involving the use of maturity stages. The use of this method suggested that as the fish became bigger for their age, they moved farther north in summer and so in the early fifties, when the herring were very big for their age, the proportion of Downs fish on the Fladen ground increased. This may well account for the high catches/effort on the Fladen and Dogger in the period 1951–4.

Subsequently, as the numbers of older fish in East Anglia have decreased, so the proportion of older Downs fish in the North Sea has decreased. Since this time the Dogger fishery has become less profitable, but the Buchan stock has increased by about three times (the first high recruit class entered the Buchan fishery in 1952). As the Buchan stock has increased, the Shetland fishery has become predominantly a fishery for Buchan spawners, and some Dogger spawners and spent Buchan fish have been found on the Fladen ground. Presumably they have always been there (as, for example, the 'ancient' fish of the 1939 and 1941 year-classes, described by Andersson, 1950) but they were detected by the methods used in this paper only during the period of abundance in the late fifties.

The estimate of mixing by the Downs stock in the northern and central North Sea is an average one, spread over a large number of years. In order to describe what has happened in a historical manner, such procedure is valid enough, but it is less useful now that the Downs stock has declined. However, we need to be able to estimate the degree of mixture year by year. For this purpose, the methods described in this paper are useless. We need samples of the spawning groups in length for age, l_1, VS and K_2, and samples of the same characters in the feeding fisheries, in order to attempt discriminatory analysis.

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PART II

The effect of fishing on the North Sea herring

D. H. Cushing

1. INTRODUCTION

Before the First World War the greater part of the North Sea catch of herring was landed in Great Britain and the larger fraction of that quantity was landed at Yarmouth and Lowestoft. Between the wars the export markets for cured herring to Germany, Russia and eastern Europe were largely lost; continental countries replaced their imports from Britain with fisheries of their own. During this period before the Second World War it was assumed that the stock of herring was not heavily fished and that the main troubles for the British fleet were economic; the latter assumption was true, but it is now doubtful whether the stock was fished lightly. The main reason for the assumption of light fishing was that the catch per unit of effort in 1918 after the First World War was not very different from that in 1913. Table 1 shows the total annual catch in tons at Yarmouth and Lowestoft and the catch per unit of effort as cwt/landing from 1907–23 at Yarmouth and Lowestoft.

Table 1. *Annual catch in tons and catch per unit as cwt/landing at Yarmouth and Lowestoft from* 1907–23

	Catch in tons	*Catch per unit of effort as cwt/landing*
1907	148 523	121
1908	181 424	106
1909	195 552	114
1910	155 784	89
1911	182 793	124
1912	237 370	125
1913	334 120	157
1915	37 587	167
1916	4 781	131
1917	28 132	168
1918	55 892	185
1919	142 210	108
1920	194 038	142
1921	111 841	68
1922	102 783	104
1923	112 160	83

The increase of stock, as cwt/landing, during the war years (shown in Table 1) was obscured by the high catch per unit of effort in 1913 of 157 cwt/landing. This figure is high because of the very strong 1908 year-class (Bjerkan, 1917) that reached its peak at five years of age in 1913; it is likely that the figures of catch per unit of effort in 1911 and 1912 were also biased upwards by the same year-class to a lesser extent as it recruited at three and at four years of age. It would be reasonable to take an average for the years 1907–12 and this works out as 113 cwt/landing (it is 119 cwt/landing for the years 1907–13). By 1917 and 1918, the 1908 year-class was 9 and 10 years old respectively: in other words, it was practically extinguished. The catches per landing in these two years were 168 and 185

cwt, an average of 177; five years later, the catch per landing had been reduced to about 100 cwt. Between the wars the catch per landing averaged about 30 crans, or 112 cwt, which is not very different from that before the First World War. Comparing the average value of 177 cwt/landing in 1917 and 1918 with that of 112 cwt/landing, which is a reasonable value for the period before the First World War and that between the wars, we find that the relaxation of fishing during the war was associated with an increase in stock of 1·58 times. This is not evidence of heavy fishing, as was recorded for the plaice and haddock by Russell (1942) for the same period, but it is evidence of the noticeable effect of fishing. This is a most important point, because as late as 1954 (Graham, 1956) the effect of fishing on the herring was considered to be low, although increasing. Table 2 summarizes these data.

Table 2. *The wartime effect on the stocks of haddock, plaice and herring*

Haddock (*English steam trawlers catch/day's absence*)		*Plaice* (*English steam trawlers catch/day's absence*)		*Herring* (*Cwt/arrival at Yarmouth and Lowestoft*)	
	cwt		cwt		cwt
1906–14	5·5	1906–13	2·6	1906–13	119
1919	15·8	1919	4·5	1917/18	176
1922–8	6·1	1922–5	2·1	1920–3	100
(Russell, 1942, Table 4 p. 30)		(Thursby-Pelham, 1939)		(Table 1 of this paper)	
War/Peace ratio in stock:	2·6		2·1		1·6

It is interesting to compare the stock densities before, during and after the First World War with the same before, during and after the Second World War. Figure 1 shows the stock densities in the East Anglian fishery from 1924 to 1962. Again an increase in stock density was found when fishing was relaxed during the war, followed by a decrease after it when fishing was restored. The War/Peace ratio [1945/1955–60] is 3·3–4·0, which implies that the effect of fishing has increased since the First World War. The effort figures used were not corrected for the efficiency change described below. It is likely that the War/Peace ratio, using stock densities based upon 'efficient' effort figures, would be considerably greater.

In 1955, the East Anglian herring fishery collapsed. After the Second World War catches had reached 50 000 to 60 000 tons per year (1947–50), but in 1955 they fell below 20 000 tons and by 1959 had fallen to less than 10 000 tons. It has become a matter of urgency to understand the causes of this decline.

The effect of fishing on the herring of the southern North Sea was studied in a preliminary way in Cushing (1959). This study of fisheries was limited in area to the southern North Sea (including the Dogger), and to the stock that spawns from Sandettié to Cap d'Antifer in November, December and January. The effort exerted on the Downs stock in the summer feeding fishery was not included in the estimate referred to above (Cushing, 1959), because the fish of the Downs stock are mixed there with those of the Bank stock and separation of the stocks was not attempted.

The estimates of catch and effort in the Southern Bight and in the northern and central North Sea are given in Appendix Table 4 and the sources of their derivation in detail in Appendix Table 3. The estimates of catch differ from those given in Table 4 of Cushing (1959) mainly because the statistics from those fisheries subsequent to the East Anglian have been added to those of the following year; the reason for this is given below. The new estimates of catch extend back to 1924 and include some data not available in the earlier paper; in order to keep the statistical adjustments to the minimum, and of the same character through the long run of years, the adjustments and corrections used in the early part of the series were maintained right through the whole period so far as was possible. This means that certain full and extensive data collected in recent years have necessarily been ignored.

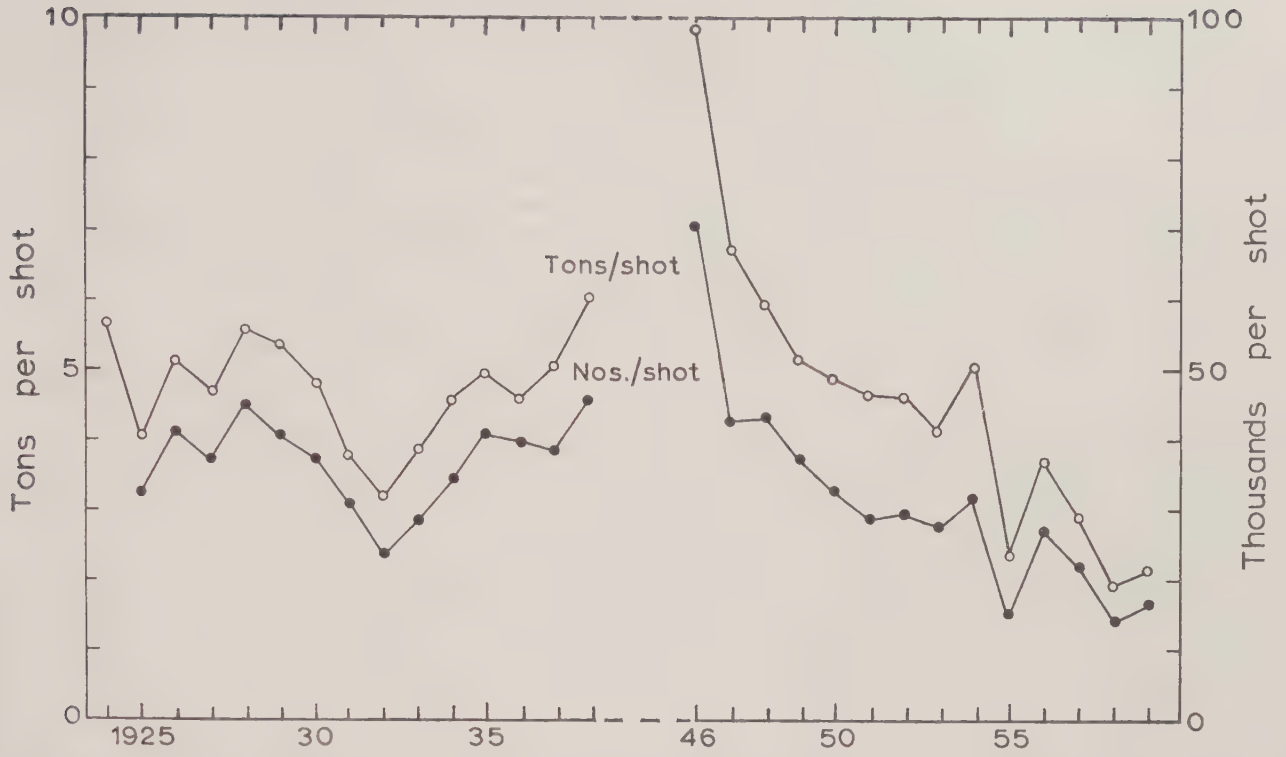

Fig. 1. *Catch per unit of effort (uncorrected for the efficiency change) in the East Anglian fishery, as tons/shot and as numbers/shot from* 1924–59.

It should be pointed out that the East Anglian fishery from Yarmouth and Lowestoft is defined as that fishery taking place on fish mainly in maturity stage V between the Norfolk Banks (lat. 53 30′N) and the Hinder and Schouwen grounds (lat. 52°N). Fish landed from north of this northern boundary in early October are often spawning fish from the Dogger spawning grounds, and fish landed from south of the southern boundary are East Anglian fish moving towards the spawning grounds at Sandettié and in the Eastern Channel. On some occasions spawning fish are landed from within this area, particularly from a ground near the Galloper lightvessel. The reasons for separating the Sandettié grounds from the East Anglian fishery proper are that fish may not pass through the spawning grounds in the age sequence in which they pass through the East Anglian fishery, and also that the fleet may concentrate more readily on the spawning grounds, producing a higher catch per unit effort on a given age group than that sampled in the East Anglian fishery. The total East Anglian catch reported in the catch statistics includes all fish landed at Yarmouth and Lowestoft; those catches from the Hinder and Schouwen grounds are included in the East Anglian catch. Those catches from north of the Norfolk Banks (north of 53°30′N) in early October were also included, comprising $4\frac{1}{2}\%$ of the total from 1924–57, of which one third (see below) may be considered as Downs stock fish, and so the total East Anglian catch was biased upwards by 3%. In 1958, and subsequently, the proportions landed from north of the Norfolk Banks were very much higher and have been subtracted from the total catches.

Since 1955, catches in the Southern Bight have fallen greatly. From the shape of the yield curve for herring (Figure 12), an increase in fishing effort should yield an increase in catch. Total mortality has remained high. For the same period a sharp increase in the efficiency of East Anglian driftermen, and a clear relationship between total mortality and fishing effort will be described. It will be shown

that since 1955 the recruitment to East Anglia has not remained steady, but has declined. This was foreshadowed in Part I and is described more fully in Part III. It is sufficient at the moment to account for the increased high mortality in the East Anglian fishery.

2. ESTIMATION OF MORTALITY RATES IN THE SOUTHERN BIGHT, AND THE EFFORT EXERTED ON THE THREE SPAWNING GROUPS (BUCHAN, DOGGER AND DOWNS)

Mortality rates in the East Anglian fishery are given in Appendix 1; they are derived from numbers/shot. The report of the Herring Assessment Group (1964) to the North East Atlantic Fisheries Commission shows that the mortality rates for ages five to seven in the East Anglian fishery correspond to those for all ages in the Channel spawning fisheries during the fifties.

In this section a bias in the East Anglian mortality is described. A short account is given of an increase in the efficiency of the East Anglian driftermen. The catches of each of the three spawning groups are given and with them the methods of deriving the efforts exerted on each of them.

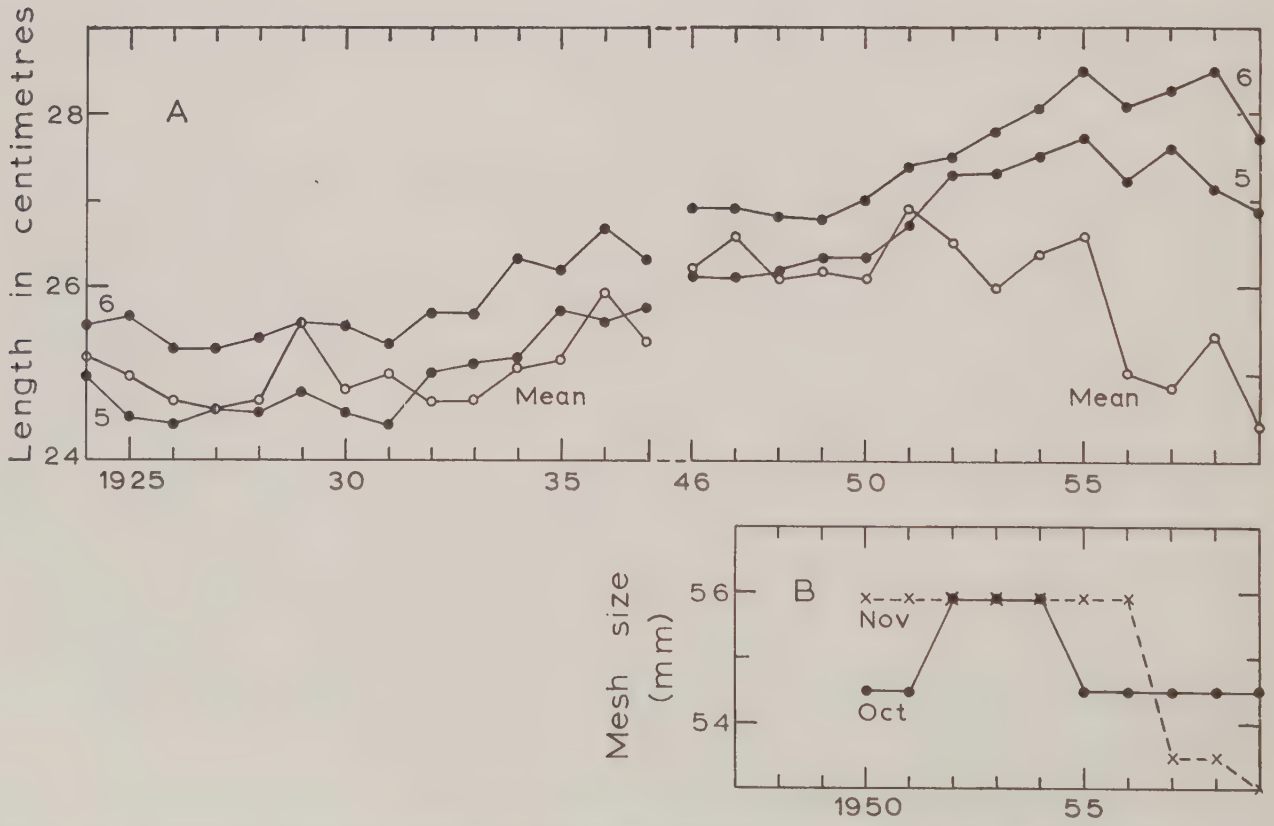

Fig. 2. A. *Length of five- and six-year-old fish and the mean length in the East Anglian fishery from* 1924–59, *excepting the years* 1938–45.

B. *Changes in mesh size in October and November to the drifter fleet of Messrs Small and Co. Ltd* (*Lowestoft*) *from* 1950–9.

A BIAS IN THE MORTALITY RATES OF THE EAST ANGLIAN FISHERY

With drift nets it is obvious that selection must occur to some degree. Hodgson's (1927, 1933) experiments with single drift nets showed sharp selectivity. On the other hand, Borley and Russell (1922) compared the length distributions of drift-caught and trawl-caught fish and found that they were very similar. This suggests that a drifter fleet is so catholic in its selection of fish that none takes place. The problem is to determine the selectivity of a fleet of drift nets rather than that of a single net. Recently, Burd (1963) has examined the problem, using an extensive series of mesh measurements in the East Anglian fleet. He showed that the selection curve of East Anglian drift nets was effective only in the upper half of the East Anglian length distribution. There is little selection apparently among the younger and smaller fish.

Figure 2A shows a time series in the length of five- and six-year-old herring and in the mean length of herring in the East Anglian fishery from 1924 to 1959. From 1928 to 1955 there was a steady increase in the length of five- and six-year-old herring, and since 1955 this trend has been reversed. (In the early sixties the herring have grown bigger for their age again; this is outside the period of catch statistics available at the time of writing, and so is not included in the present analysis.) The trends in mean length follow the same sort of pattern, but since 1955 there has been a sharp decline with the disappearance of the older fish. During the East Anglian fishery, because of the age sequence in time (Hodgson 1939), the drift nets were changed at the end of October to catch the larger fish in November. When large stocks of nets were available, as before the Second World War, adjustments of mesh size were made very quickly almost as the fishery proceeded. After the war, the changes in mean length of the fish were greater and the real change in mesh size was often made a year later because new nets had to be bought. If mesh size were altered with the changing mean length of the herring, one year later, mortality rates might become biased. Figure 3 shows a regression of the increments of length from five to six years of age on the deviation of total mortality in the age pairs 5 to 6 from that in the age pairs 5 to 9. Here it was assumed that Z_{5-6} was more sensitive to the increments of length from 5 to 6 years of age than Z_{5-9}. The regression was calculated in two parts, 1925–38 (crosses and a broken regression line) and 1946–58. The full line represents all observations from 1924 to 1958. Table 3 gives the statistical results.

Table 3. *Regressions of* Δl_{5-6} *on deviations of* Z_{5-6} *from* Z_{5-9}

	1925–38	1924–58
Intersect, *a*.	0·896	0·862
slope, *b*.	0·350	0·361
Probability that the slope is not different from zero	0·1	0·04
Number of observations	13	25

Hence the greater the increment in length from five to six years of age, the greater the deviation of the mortality rate, Z_{5-6}, from that of Z_{5-9}. So variation in mortality rates can be directly associated with the changes in growth rate.

The more important point, however, is whether the magnitude of the mortality rate can be affected by changes in the growth rate. Figure 4 shows regressions of the increment (or decrement) of mean length on the mortality as estimated between the five- and seven-year-old fish in a year-class. During the pre-war period, when nets were changed within a season, the increment of mean length is related to the mortality rate in the same pair of years. In the post-war period, when nets were changed between seasons, the increment of mean length is related to the mortality rate in the subsequent pair of years. The data are summarized in Table 4.

Table 4. *Regressions of increments of mean length (Δl) on Z_{5-7} for different periods*

	1924–37	1925–38	1946–59	1947–59	1924–37 1947–59
	Δl on Z_{5-7} in same year-pair	Δl on Z_{5-7} one year later	Δl on Z_{5-7} in same year-pair	Δl on Z_{5-7} one year later	Δl on Z_{5-7} in the same year-pair, 1924–37 and Δl on Z_{5-7} one year later
a	0·473	0·162	0·067	0·394	0·387
b	−1·092	−0·324	−0·106	−0·737	−0·793
p	0·01	0·45	0·8	0·07	0·01
n	12	13	12	11	24
	Figure 4A	4B	4C	4D	4E

Mr Victor Bond, the net manager of Messrs Small and Co. of Lowestoft, has told me that the biggest nets were put in the boats in November in the pre-war period. Figure 2B shows the changes in mesh size in the drifter fleet belonging to Messrs Small and Co. The nets have a specified mesh size, as made in a given year. Imperial Chemical Industries have prepared a relationship between age and shrinkage of wet nets and so it was possible to specify the average mesh size of Small's fleet

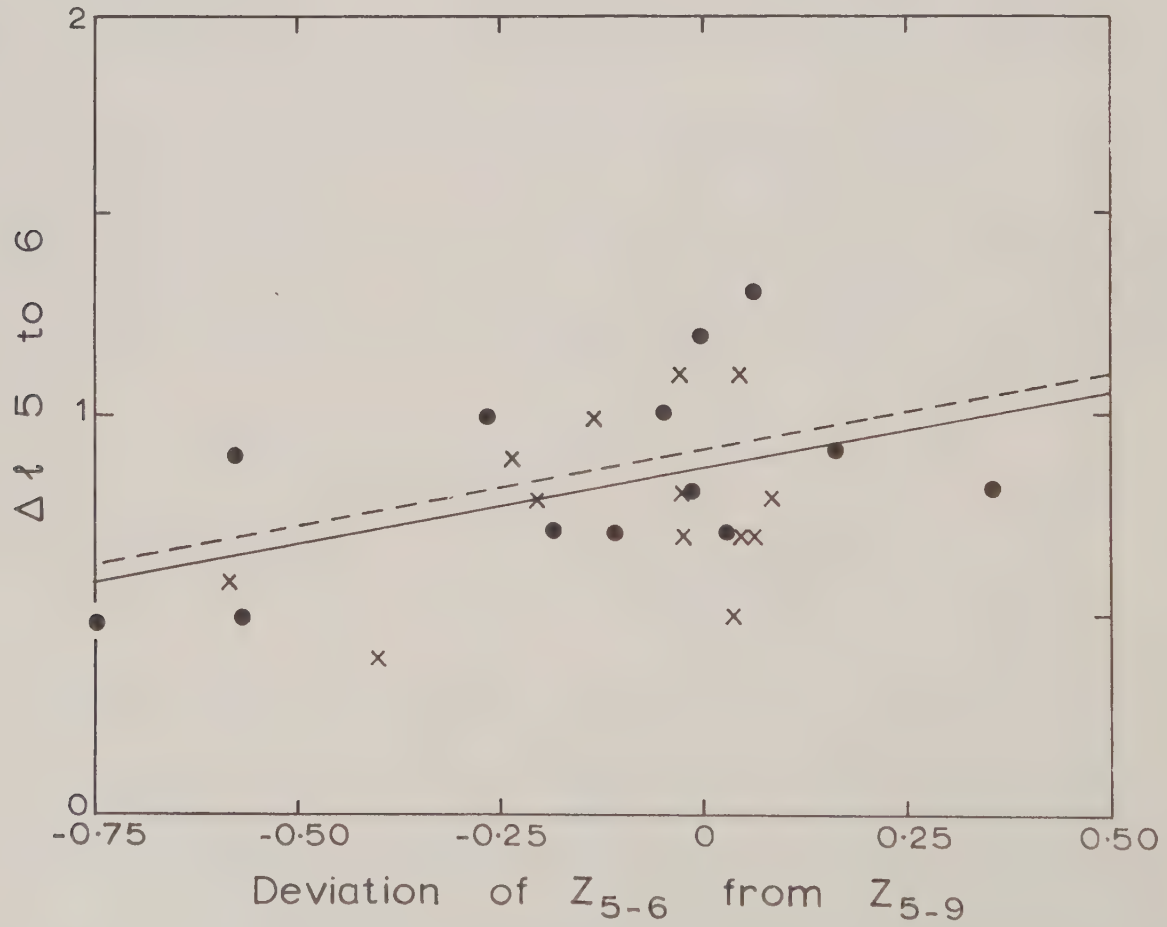

Fig. 3. *Regression of* Δl, *the increment of length, from five years of age to six, in year-classes, on the deviation of* Z_{5-6} *from* Z_{5-9}. *The crosses represent the data from the pre-war period, and the circles the data from the post-war period. The broken line is the regression for the pre-war data; the full line is the regression for all data, which is significantly different from zero.*

of nets in mm. In Figure 2B they are plotted as a time series on the same scale as the length data. The increase in mean length in 1951 is followed by an increase in mesh size a year later in October 1952, and the decrease in mean length in 1956 is followed by a decrease in mesh size in November 1957. The decrease in October 1955 is not to be accounted for in this way. But there is some evidence that the response of the driftermen to the changes in mean length comes a year late in the post-war period. The most important point, however, is that the mortality rates can be biased considerably by selection, as expressed in the change of mean length. A positive increment in mean length of 0·4 cm can reduce the mortality rate to less than zero and a decrement of 0·5 cm can increase the mortality rate by 0·6. Increments (or decrements) of this order occurred about ten times in the time series given in Figure 2.

Such a correlation as that shown in Figure 4 can only be simply explained if the selection curve is effective only on the bigger fish; in other words it is an ogive, like a trawl mesh selection curve in reverse. If it were a bell-shaped curve, the effect of a change in length on mortality would be very difficult to disentangle. An increase in mean length causes an underestimate of stock in the first year of the mortality pair. Then new nets are put in the following year and stock is correctly estimated but the mortality rate between the two years is biased downwards. If the selection curve were a bell-shaped one, the effect would be reversed on the mortality rates of the younger age groups. When a decrease in mean length takes place, I believe that in the first year of the mortality pair stock is correctly estimated. Then the reduced size of drift nets in the following year is an over-correction and mortality rate is biased upwards. This concept is in agreement with Burd's findings (1963) and would explain the basis of the correlation in Figure 4.

The relationship shown in Figure 4 is worth pursuing only so long as there is no regression of the increment of mean length on effort. None would be expected, but in general both have been increasing during the same period in the North Sea and so such a regression could arise by chance. When tested, none was found ($p = 0{\cdot}8$; $n = 24$).

The regression fitted to the data in Figure 4 is Δl (the increment of mean length) on Z (the instantaneous coefficient of total mortality). It is then possible to estimate ΔZ from Δl. This bias to the mortality rate can then be added to or subtracted from the observed mortality rate. The effect of the bias in a regression of mortality on effort is shown in a later section.

In the equation $\Delta l = a - bZ$, the error on bZ is that on Δl. Table 5 shows the standard errors of adjusted mortality for a range of effort values, based on the error of Δl.

Table 5. *The coefficient of variation in adjusted mortality rates as derived from the error in the increment of mean length, for a range of values of fishing effort* (g)

g. (number of drifter shots)	$2{\cdot}10^4$	$4{\cdot}10^4$	$6{\cdot}10^4$	$8{\cdot}10^4$	$10{\cdot}10^4$
Coefficient of variation	151%	90%	64%	51%	42%

NOTE: The coefficient of variation was estimated from $\dfrac{Syx\sqrt{1 + 1/n + Sx^2/Sxy}}{x}$

where Syx is the standard deviation about regression;
where x is the deviation of the adjusted value of Z from the mean;
where Sx^2 is the sum of squares of deviations from the mean of mortality rates;
where n is the number of observations.

The important point here is that the coefficient of variation is high, although it decreases with increasing effort. In other words, having adjusted the mortality rates there is a high component of variance.

Table 6 shows the results of an analysis of variance carried out on the regression of adjusted mortality rate on effort.

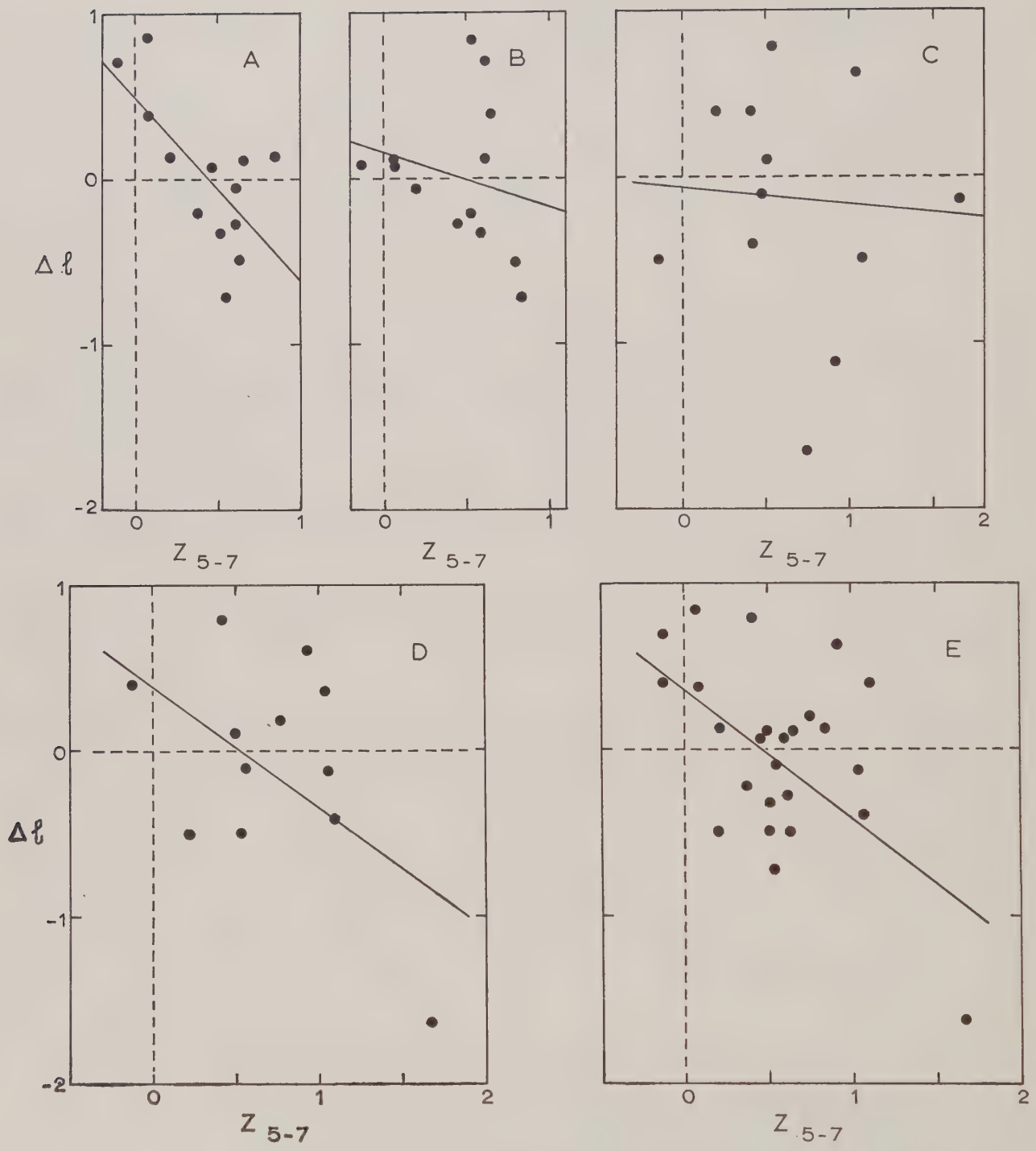

Fig. 4. *The effect of changes in mean length on the mortality rates.*

A. *Regression of* Δl, *the increment of mean length, on* Z_{5-7}, 1924–37, *the increment being in the same year as the mortality pair.*

B. *Regression of* Δl *on* Z_{5-7}, 1925–38, *the increment being one year earlier than the mortality pair.*

C. *Regression of* Δl *on* Z_{5-7}, 1946–59, *the increment being in the same year as the mortality pair.*

D. *Regression of* Δl *on* Z_{5-7}, 1947–59, *the increment being one year earlier than the mortality pair.*

E. *Regression of* Δl *on* Z_{5-7}, 1924–37, *the increment being in the same year as the mortality pair, and* 1947–59, *the increment being one year earlier than the mortality pair.*

The regressions in Figure 4*A, D and E are significantly different from zero* ($p = 0{\cdot}01$, $0{\cdot}07$ *and* $0{\cdot}01$ *respectively*).

Table 6. *Analysis of variance on the regression of adjusted mortality rate on effort*

	Sums of squares	*Degrees of freedom*	*Mean square*
Deviations determined by the slope	0·868	1	0·868
Random deviations	3·322	22	0·151

$F = 5{\cdot}75$, which is significant between the 5% and 1% levels.

We may use the mean square to calculate the error on any single estimate of mortality; it is 0·39. As the mean is 0·74, this is rather a large proportion of the mean – as is inevitable from the facts given in Table 5.

Summarizing, we may conclude that the raw mortality rates as estimated in the East Anglian fishery are biased downwards when mean length increases and upwards when mean length decreases. The error about the regression of mean length on mortality rate is high. It must be considered possible that the bias cannot be fully removed, or is removed inefficiently.

A CHANGE IN THE EFFICIENCY OF THE EFFORT EXERTED BY THE EAST ANGLIAN DRIFTER FISHERY

Cushing (1959) tried to estimate changes in efficiency, using the estimates of catch and catch/effort in small statistical squares. Necessarily such an estimate is limited to information between squares. However, it is likely that any increase in efficiency is based on 'within square' information, for example, as a consequence of searching by echosounder, whereas an efficiency change based on 'between squares' information might be an effect of improved radio communication. It is not thought that echo searching yields only 'between square' information. It is, however, thought that the earlier method of estimating the efficiency changes described in Cushing (1959) need not describe them fully.

Figure 5 shows a second attempt to estimate the efficiency changes, using a ratio of catch per shot to stock. Catch per shot was expressed as numbers per shot. Stock was also expressed in numbers. The measure of stock was obtained in the following way: the catch of each age group in weight was divided by the weight for age of that age group to give catch in numbers; such catches were summed for all ages and the sum raised by $\frac{Z}{F} \cdot \frac{1}{(1 - e^{-z})}$.

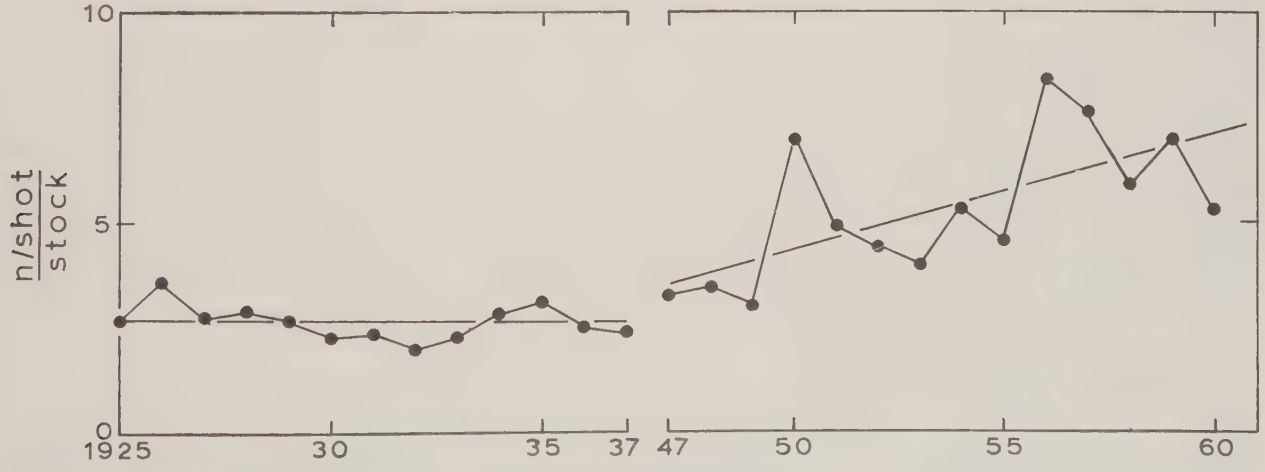

Fig. 5. *The change in efficiency of East Anglian driftermen. Stock density in numbers/shot is expressed as ratio to stock in numbers, based on Downs catches.*

Let $N = C \cdot \frac{Z}{F} \frac{1}{(1 - e^{-z})}$,

where N is stock in numbers;

where C is catch in numbers, 'Downs' catch being used;

where Z is the instantaneous coefficient of total mortality;

where F is the instantaneous coefficient of fishing mortality.

Catch per shot in numbers may be represented as $\frac{C}{g}$, where g is effort. Then the ratio used is

$$\frac{C}{g} \cdot \frac{qg}{C} \cdot \frac{(1 - e^{-z})}{z} \text{ or } q \cdot \frac{(1 - e^{-z})}{z}.$$

Total mortality has doubled during the period (from 0·5 to 1·0), so $(1 - e^{-z})/Z$ has increased from 1·33 to 1·50. Thus the ratio is biased upwards by 10% between 1947 and 1960. Similarly, if mortality is based on ratios of catches/effort from year to year, it can be shown that the estimate of mortality is biased upward by 7% – which reduces the first bias slightly. Figure 5 shows a time series of the ratio of stock density to stock from 1925 to 1960, uncorrected for the small upward bias during the post-war period. There is no upward or downward trend in the pre-war series, but there is a marked upward trend post-war. The line is fitted to the post-war series and the pre-war mean. The efficiency factor for post-war effort is taken as being the ratio of any post-war observation from the fitted line to the pre-war mean. The nature of the efficiency change is unknown. It should be pointed out that the ratio $\left(\frac{n/\text{shot}}{\text{stock}}\right)$ increases more sharply in the post-war period if catches from the Southern Bight only are used to represent the Downs stock.

CATCHES OF HERRING IN THE NORTH SEA AND THE EFFORT EXERTED ON THE THREE SPAWNING GROUPS

From the estimates of mixing given in Part I, it is possible to allocate proportions of catches to the different stocks. The figures are given in Appendix 2. Each of the three stocks has a separate and distinct spawning ground upon which a specific gear operates. For example, trawl catches on the Downs spawning ground would represent a firm base for the calculation of effort. However, they did not start in quantity until the fifties, whereas statistics of the East Anglian drift-net fishery are available from 1924 onwards. In the late fifties the East Anglian fishery formed but a small part of the total catch and to raise the East Anglian effort by the ratio of total Downs catch to East Anglian catch introduces error into the system, but bias is unlikely. The same is true for the Buchan spawning fishery which formed a small proportion of the catch of the Buchan stock in the Buchan pre-spawning fishery, and in the Fladen, Shetland and Viking Bank fisheries. In the case of the Dogger spawning fishery that proportion of the Dogger fishery is used which is not accounted for by the East Anglian mixing rate. Summarizing, effort estimates derived from catch ratios are based on the East Anglian fishery for the Downs stock, on the October Dogger fishery for the Dogger stock and on the Buchan spawning fishery for the Buchan stock.

There is one fishery that provides some difficulty – that on the Viking Bank in spring. With the use of average proportions of spring spawners, the Norwegian spring-spawning catch can be separated. There is not yet sufficient information to attempt a separation of Buchan and Dogger spawners. So blandly and with no evidence I have allotted one half to the Buchan stock and one half to the Dogger spawning stock.

Before we examine the effort exerted on the three stocks, information on catches per effort and on age distributions have to be extracted from the original publications. Catches have not been reported in the same way for all areas from 1924–60; in fact, the separation of catches has been a laborious and complicated task, which has been carried out for me by Mrs Berry. Large quantities of information have been neglected because they extend for only short periods of time; we have tried to use the same statistics throughout the whole period, in preference to successive sets, each of which might be of better quality than the long series. The sources of data are set out in Appendix Table 3.

The catches of herring in the North Sea in the various named fisheries (as for example Fladen, Dogger etc.) from 1924 to 1960 are given in Appendix 4; they are taken from the publications listed in Appendix 3. The catches in Appendix 4 are split according to the stock proportions (from Part I) given in Appendix 2. Effort for each of the three stocks is derived by raising the effort on the stock in the spawning fishery by the ratio of total stock catch to the catch from the spawning fishery.

3. THE ESTIMATION OF FISHING MORTALITY AND OF NATURAL MORTALITY

FIRSTLY will be given estimates of natural mortality from wartime 'catch curves', and estimates of fishing mortality based on the ICES Bløden tagging experiment (Aasen et al., 1961) and on the French tagging experiment (Ancellin and Nédelèc, 1959). Secondly, the relation between mortality and effort will be examined for the Downs stock. Lastly, the relationship between catch/effort on effort for each of the three spawning groups will be examined.

ESTIMATES OF NATURAL MORTALITY AND OF FISHING MORTALITY

Gilis (1957) has published age distributions of the Belgian spent herring fishery during the war in two periods, 1939–40 and 1941–6. Andersson (1949) has published an age distribution from the Fladen fishery in September 1946. Ancellin (1948) gives an age distribution from the Boulogne fishery in the autumn of 1945. Age distributions of North Sea Bank herring in the Bohuslän fishery during the First World War are given by Andersson (1958). At the end of either war, age distributions below a certain age should be free from the effect of fishing and so the mortality rate expressed in a catch curve then (Ricker, 1958) should be due to natural causes only. Percentage age distributions can be used for this purpose, and so the marked availability changes found, for example in the Belgian spent fishery during the Second World War, can be avoided.

Considering the age distributions available during the Second World War, we assume that recruitment was complete by five years of age and that fishing in the winter of 1939–40 was reduced. Then by 1944 the whole age distribution from five to ten years of age is free from the effect of fishing. In 1941, the eight-, nine- and ten-year-old fish had suffered fishing as fives, sixes and sevens in 1938 (and in earlier years). The ten-year-olds had spent 3/7 or 3/8 of their exploitable lives under conditions of no fishing, and for the eight-year-olds this fraction was 4/5 or 4/6. In the total age distribution from five to ten years of age, this amounts to a little more than one year in six. Therefore the age distributions from 1941 onwards will yield overestimates of natural mortality. Table 7 gives the total mortalities in three fisheries during or at the end of the Second World War.

Table 7. *Total mortalities from catch curves (based on percentage age distributions) during and just after the Second World War*

Belgian spent herring fishery			*Boulogne fishery*	*Fladen fishery*
1941/2	1942/3	1943/4	1945	1946
0·32	0·21	0·13	0·22	0·17

For the catch curves in the Belgian spent herring fishery during the war, Postuma (1963) has given a value of $M = 0{\cdot}08$; this was rather a fuller examination of data than that given in Table 7.

The grand mean of these estimates is 0·20. It is interesting that the only estimate from the First World War, the percentage age distributions of the Bohuslän fishery on North Sea Bank herring from 1913–21 (Andersson, 1958), yields a total mortality of 0·20–0·25. Again, Burd and Bracken (1965) have shown that the best estimate of natural mortality in the Dunmore fishery is 0·15, using a regression of total mortality on effort. There is a considerable consistency about these estimates of natural mortality of herring. With the exception of the Dunmore estimate, they are all wartime estimates, when with high abundance, one would expect that the opportunities for parasitism and disease were greatest. If cod were predators, it is also likely that they were more abundant during the war than before or afterwards.

Two methods are available for estimating fishing mortality: firstly, indirectly from the Bløden stock, as estimated in the ICES tagging experiment (Aasen et al., 1961) and secondly, directly from the French tagging experiment (Ancellin and Nédelèc, 1959).

From the ICES tagging experiment, it was estimated that there were 420 000 tons of I-group stock in the 1955 year-class. In 1958, these fish joined the adult fisheries as three-year-old recruits. Between the Bløden ground and the Southern Bight, the fish grow by more than two times in weight, suffer natural mortality, and segregate to different adult stocks. In theoretical calculations of fishing mortality, natural mortality is set at $M = 0{\cdot}1$, 0·2, 0·3 or 0·4, and the proportions of potential Downs recruits in the Bløden stock are set at 0·2, 0·3, 0·4 and 0·5. The numbers of fish per ton are known on the Bløden ground (Cushing, 1959) and in the adult fisheries in the North Sea. Within these conditions and facts we also have the stock on the Bløden ground and the catch in numbers of three-year-old fish in the Southern Bight, together with estimates of total mortality. Knowing the ratio of catch to stock, it is possible to estimate the fishing mortality from:

$$F = \frac{\text{Catch} \,.\, Z}{\text{Stock} \,.\, (1 - e^{-z})}$$

where Z is the total mortality of three-year-old fish during the year.

The complete calculation is illustrated in Figure 6 in which F, fishing mortality, is plotted on the Downs proportion at different levels of Z. Separate figures are given for the four levels of possible pre-recruit natural mortality, M'. Table 8 summarizes the estimates of fishing mortality.

Table 8. *Estimates of fishing mortality from the ratio of Southern Bight catch to the Bløden stock, with some restrictions*

	Pre-recruit mortality (M')					
	0·20		0·30		0·40	
Downs proportion	0·35	0·50	0·35	0·50	0·35	0·50
Catch in numbers: $786 \cdot 10^6$	0·55	0·38	0·60	0·41	0·66	0·46

1. $Z = 0{\cdot}8$.
2. A rough estimate of the Downs proportion can be taken from Figure 5 in Cushing (1959) (in this paper, Figure 7). This Figure relates $L/(L + N_3)$, as percentage (where L is the number 'lost' or caught in the Bløden fishery and N_3 is the number of recruits reaching the Southern Bight), to catch in tons from the Bløden fishery, at different levels of Downs proportion. The ICES tagging experiment gave a 15% 'loss' from stock of the 1955 year-class on the Bløden ground. Figure 7 shows that with a catch of 75 000 tons (60 000 tons of I-group fish in the autumn of 1957 and 15 000 tons of II-group fish in the spring of 1958) and a loss of 15%, the Downs proportion is 0·35. It is larger with less catch and larger with higher loss rate.

With a Downs proportion of 0·35, $F = 0{\cdot}55$–0·66; with a Downs proportion of 0·50, $F = 0{\cdot}38$–0·46. The likely values of M' are = 0·3 to 0·4, with the Downs proportion at 0·35, so $F = 0{\cdot}55$–0·66. If anything, M' should be higher than $M = 0{\cdot}20$ and the Downs proportion may be less than 0·35, so

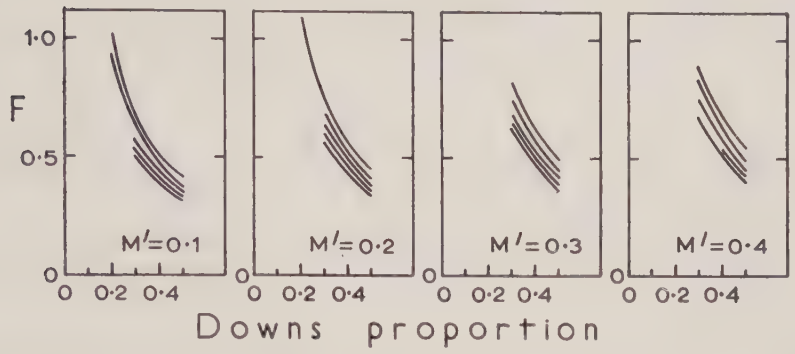

Fig. 6. *Calculations for the estimation of fishing mortality from the Bløden tagging experiment* (*Aasen et al*, 1961). M′ *represents the pre-recruit mortality.*

the average value of F will be a little greater than 0·55. With $Z = 0{\cdot}80$, $M = 0{\cdot}20$–$0{\cdot}25$, which is the same conclusion obtained by a quite independent method. The importance of this method is that it yields not a wartime estimate, but one in the late fifties. Hence it is possible that natural mortality has not changed much during the period.

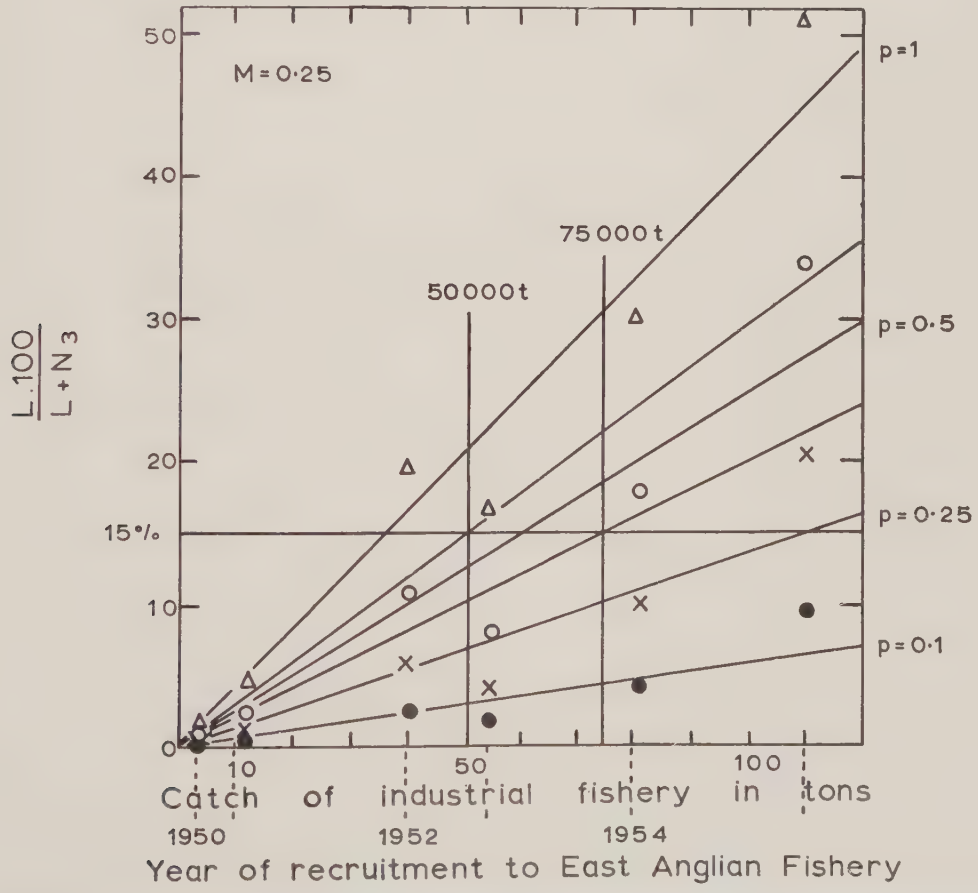

Fig. 7. *The loss of recruitment to the Downs stock as a function of the Bløden catch, for various proportions of the Downs stock in the Bløden fishery* (*Cushing*, 1959).

The experiment described by Ancellin and Nédelèc (1959) was carried out on the herring trawling grounds in the Straits of Dover and in the eastern English Channel in November 1957. These authors showed that the effect of fishing amounted to 1·2% fishing mortality per day; as the fishery lasted intensely for 10–12 days in each area of tagging, it is likely that the fishing mortality amounted to 15% in this fishery.

It was shown that the fishery lasted for 10–12 days on each of the five areas, Sandettié, Blanc Nez, Vergoyer, Dieppe and Ailly; the whole fishery over the whole area lasted for 24 days. If each area were a completely separate fishery, the effective duration would be 10–12 days; if there were full interchange between each area, the effective duration would be 24 days. Because fish swim through the Sandettié, Blanc Nez and Vergoyer grounds in order to spawn at Dieppe and Ailly, it is likely that the true duration lies between 10 and 24 days. 77% of tags recaptured were taken on the grounds of liberation; as the rate of return decreased very quickly (particularly at Sandettié and Blanc Nez), it is possible that as a measure of localization to banks this proportion is too high. 13–15 days is then a minimum effective duration, with 17 days $\left(\frac{10+24}{2}\right)$ being possibly a realistic estimate.

Figure 8 shows the number of tags returned, plotted logarithmically on a time series for each ground. The linear decline in the number of tags returned can be used to estimate fishing mortality, using the formula given in Beverton and Holt (1957):

$$F = \frac{\frac{n_1}{\tau} \log_e \frac{n_1}{n_2}}{N_0 (1 - n_2/n_1)}$$

where N_0 is the number of tags released;

where τ is the unit period in which tags are recovered;

where n_1 is the number recovered in the first period of τ days;

where n_2 is the number recovered in the second period of τ days;

where F is the instantaneous coefficient of fishing mortality.

Table 9 gives the results as fishing mortality for 10 days and 24 days respectively for each tagging area and for the whole region.

Table 9. *Estimates of fishing mortality from the French tagging experiment (Ancellin and Nédelèc, 1959) for durations of 10 days and 24 days*

	F (10 days)	*F* (24 days)
Sandettié	0·034	0·082
Blanc Nez	0·071	0·170
Vergoyer	0·058	0·139
Ailly	0·031	0·074
Average	0·048	0·116

In 1957, the East Anglian effort amounted to 5 013 shots. The Channel catch was 51 190 tons, as compared with 21 160 tons at East Anglia; the Downs catch amounted to 229 055 tons and so the Downs/Channel catch ratio is 4·48. So the estimated fishing mortality, using a 17-day estimate, is $0{\cdot}082 \times 4{\cdot}48 = 0{\cdot}38$. This value depends upon the estimated duration of the fishery; the figure used is that derived from the duration of the tagging experiment. Table VII of Ancellin and Nédelèc shows that tags were being recovered a month after the start of tagging on the Vergoyer. Such a

duration would give an estimated F of 0·65. For the period 1957–8 the average effort was 75 700 shots, which gives a fishing mortality of 0·41, using the 17-day estimate. Given that $Z = 0{\cdot}80$ the apparent value of M is 0·39. For the reasons given above this is an overestimate; it would be fair to use a maximum value of 0·35.

These are four estimates of natural mortality:

(*a*) 0·20, from wartime estimates;

(*b*) 0·225, from the Bløden stock estimates;

(*c*) 0·15, from the Dunmore fishery investigations (Burd and Bracken, 1965);

(*d*) 0·35, from the French tagging experiment.

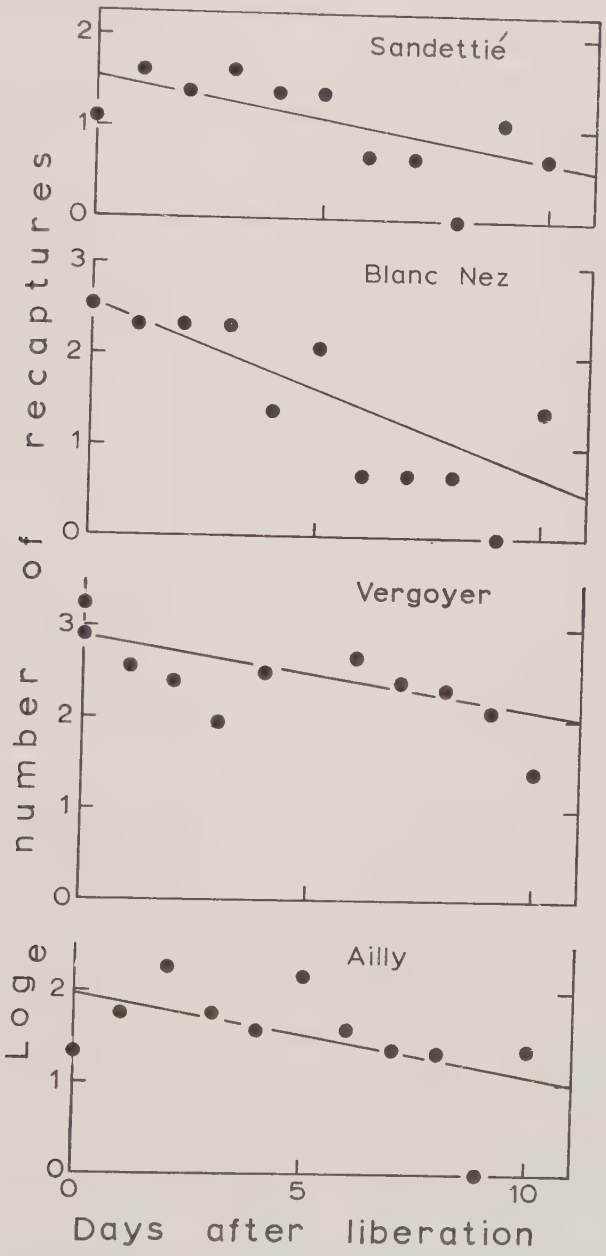

Fig. 8. *The loss of tag recaptures (in logarithms), on time on each of the four grounds of liberations during the French tagging experiment (Ancellin and Nédelèc, 1959).*

If Z is high, 0·95 in the Downs stock (Appendix Table 1) and probably about 0·75 (Herring Assessment Group Report, 1964) in the Buchan stock, it is likely that fishing mortality in the North Sea herring is high – as much as 0·50 in the north and 0·70 in the south.

THE RELATION BETWEEN MORTALITY AND EFFORT

In Appendix Table 1 are given the mortality rates by age pairs in the East Anglian fishery from 1924–60; these include the data as given in Cushing (1959), with two changes. From 1924 to 1928, percentage age distributions have been raised by the average catch per unit effort (catch/landing $\times$ 1·24, to convert it to catch/shot). From 1956 to 1960, a set of mortality rates is added to the series, estimated from the numbers/shot of each age group. Burd (1964) has published mortality rates for the period 1956–62 estimated from combined Dutch and East Anglian data, expressed as numbers/net/shot; the catch per effort data in this series are also weighted by catches.

Because of the long-term nature of the recruitment change from 1925 to 1952 (Cushing and Burd, 1957), the only mortality rates free (over the whole period) of bias due to recruitment are those of fish aged five to six years and older. Since 1952, recruitment was probably complete by three years of age, but in 1925 it is likely that some recruitment took place at five years of age. Burd (1963) has considered that the effect of selection of fish smaller than 28 cm is probably not of great importance; comparison of length distributions taken by the East Anglian drifters and by the Sandettié trawlers shows a higher proportion of trawl-caught fish larger than 29 cm. By 1955–9 the age groups 5, 6, 7 and 8 are uncommon and it might be considered more proper to use the abundance of fully recruited age groups 3, 4 and 5. So with some reservations about the effect of selection on the mortality rates, as noted in an earlier section, it is thought that those calculated from the age groups 5 to 7 represent the best estimates throughout the whole period.

In Cushing (1959), the effort was related to the first year of the mortality pair. The East Anglian herring stock is sampled at the end of the year and so it is the effort during the subsequent year which reduces the stock by the following autumn. So all estimates of effort exerted after the East Anglian fishery in the same year were added to those of the following year. By comparing mortality rates with effort estimates in time series, the best correlation was found, relating mortality to effort in the second year of the pairs of years.

The first regression of total mortality on effort (Cushing, 1959) was based on Southern Bight effort (and a fraction of Dogger effort), but the effort figures were related to the first year of the mortality pair and not to the second. Figures of effort differ slightly from those then published, because of the addition of effort after the East Anglian fishery in the same year to that of the following year. Again some minor amendments have been made as a more complete survey of the available data has been achieved. Figure 9 shows the relation between total mortality, Z (corrected for the efficiency change) and the effort exerted on Downs stock through the North Sea, g_1 (corrected for the efficiency change). The proportions of effort from the mixed fisheries outside the Southern Bight are taken from Appendix 2, in turn from Cushing (in press). The figure shows clear (and significant) correlation between mortality and effort, but the estimate of natural mortality is negative.

Zijlstra and Postuma (1963) have averaged catches per effort from four areas in the North Sea; from these they calculate mortality rates and correlate them with the total effort exerted in all the North Sea. They find a high and significant degree of correlation. They also find negative values of M. Because their estimates of effort are predominantly of trawl effort, it is unlikely that the bias in total mortality associated with changes in mean length, due to selection, could produce this result. Hence there may be an undetected change in efficiency.

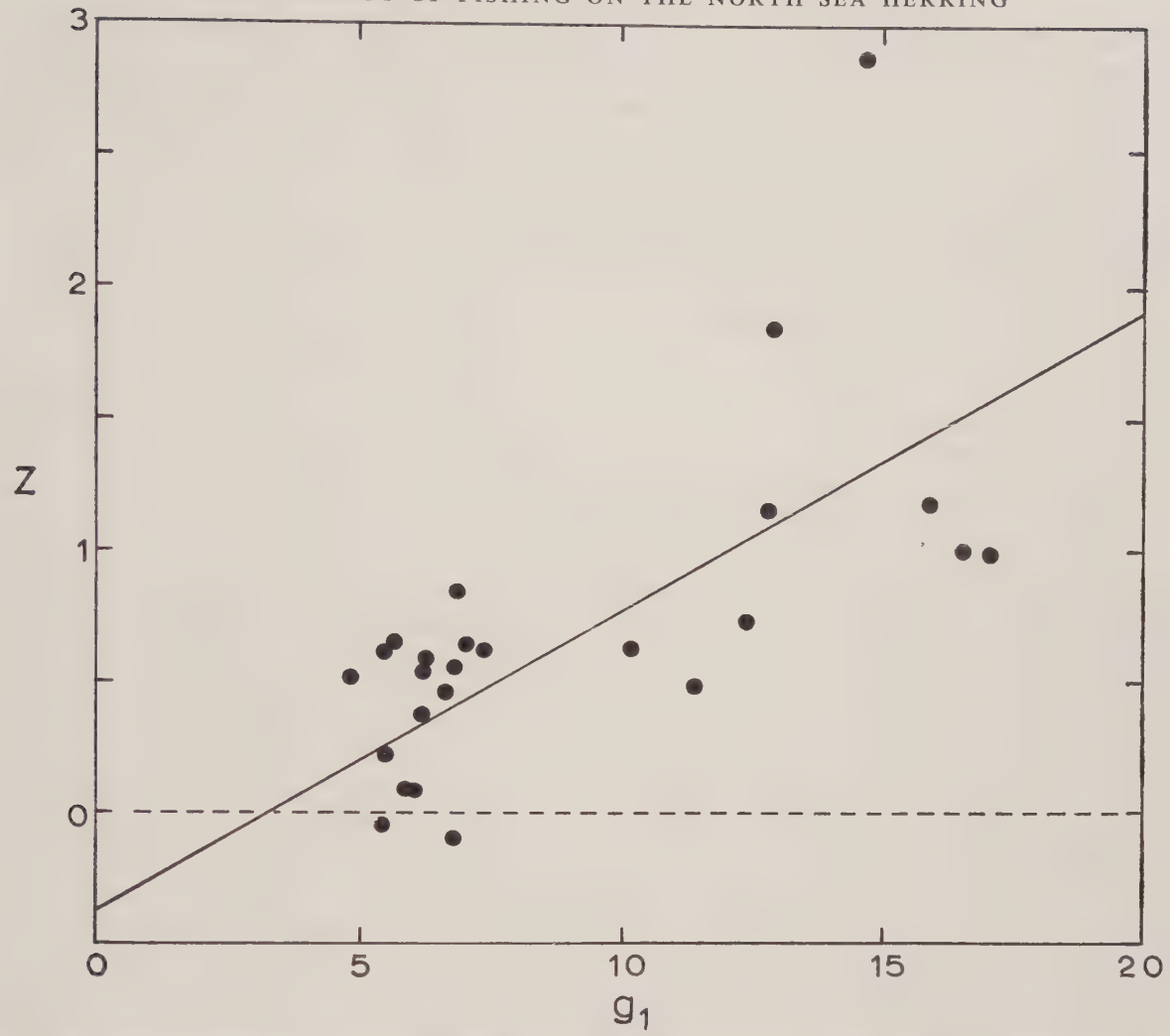

Fig. 9. *The relation between total mortality* (Z) *and the total effort exerted on the Downs stock* (g_1), *both mortality and effort being corrected for the efficiency change.*

Table 10. *Regressions of mortality on effort; Z is the raw mortality rate and Z adj. is that adjusted for changes in mean length; effort is based on North Sea catches and upon Southern Bight catches;* g_1 *is that effort raised by the efficiency factor*

	Z		*Z* adj.	
	M		*M*	
Southern Bight effort	1·6 (slope negative)	*p* 0·03	1·21 (slope negative)	NS
Southern Bight effort (g_1)	−0·02	NS	0·03	NS
North Sea effort	0·26	NS	0·05	NS
North Sea effort (g_1)	−0·18	*p* 0·05	0·085	*p* 0·05

NS = not significant.

NOTE: Where the efficiency factor has been used to raise the effort values, so the catches/effort have been corrected from which total mortality rates have been calculated.

If a true change in efficiency has taken place, then not only should the effort itself be adjusted, but also the values of total mortality, being ratios of catch per effort. Figure 10 shows the relation between Z adj. (adjusted firstly for changes in mean length and secondly for efficiency changes) and g_1, effort raised by the efficiency factor of Figure 5 for the period 1947–60. The regression is significantly different from zero ($p < 0{\cdot}05$) and the estimate of M is 0·09.

Table 10 gives a number of regressions of total mortality on effort, taking into account the mixture of the Downs stock in the northern and central North Sea (North Sea), the bias in the mortality rates (Z adj.) and the change in efficiency (g_1).

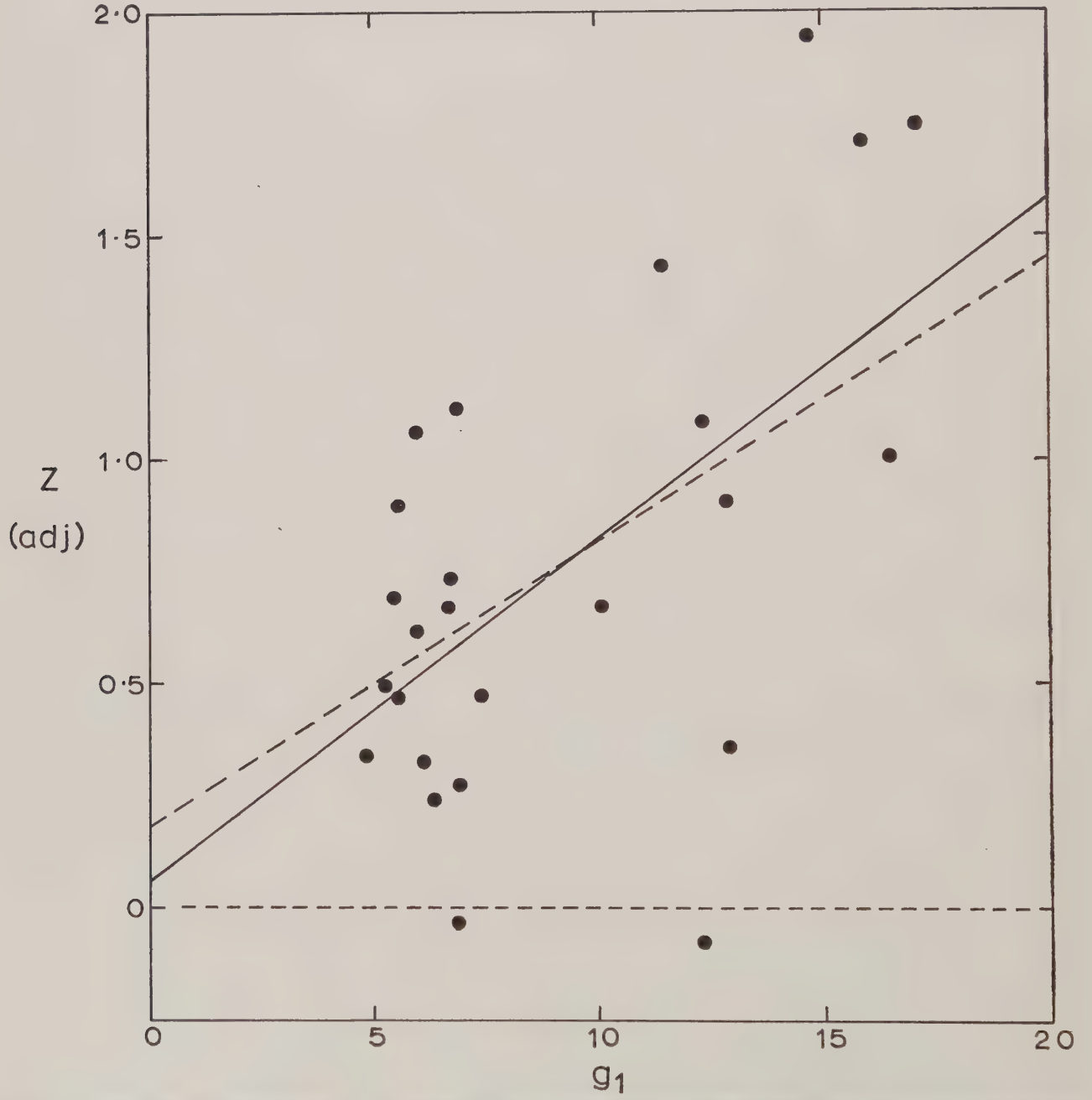

Fig. 10. *The relation of total mortality,* Z_{adj} *(adjusted for the bias associated with mean length, and corrected for the efficiency change) on the total effort exerted on the Downs stock,* g_1 *(also corrected for the efficiency change).*

The table shows that the reduction of the bias in total mortality rates associated with mean length, (Z adj.), the addition of effort from the northern and central North Sea (North Sea), and the use of the efficiency factor (g_1) have all contributed to the final regression given in the bottom right-hand corner of the table. All three steps, each of which is justified independently, are shown to be necessary ones. There are three conclusions to be drawn from these data:

(i) that fishing effort has a significant effect on the total mortality of the Downs herring stock;
(ii) that the proportion of the Downs stock mixing in the northern and central North Sea, which suffers fishing mortality, must be fairly high;
(iii) that the natural mortality of the Downs stock must be comparatively low, unless the mixing rates and efficiency factors have been underestimated.

THE RELATION BETWEEN STOCK AND EFFORT IN THE THREE NORTH SEA SPAWNING GROUPS

As fishing effort increases the stock decreases. The catch per unit of effort represents the effect of fishing effort through the average duration of a year-class in the fishery. Effort is averaged for a period which is half the average duration of a year-class in the fishery, as in Gulland's method (1961). The relation of stock on fishing effort is a curvilinear one, but within the stock ranges found in fisheries a linear fit to the data is often sufficient. It should be emphasized that the estimates of effort averaged in a running mean are not independent of each other. Using the data in Appendix 2, the mixing rates can be used to separate the catches of North Sea herring of the three spawning groups.

The relation of stock on effort for the Downs group is based on tons/shot in the East Anglian fishery and on two-year running means of effort values. Three mixed fisheries were separated: Fladen, 30% (1925–50), 50% (1951–4), 19% (1955–60); Dogger, 30% (1925–50), 50% (1951–60); Buchan, 44% (1925–50), 27% to 7% (1951–4), 5% (1955–60).

The catches in these series were added to those from the Southern Bight to give the total Downs catch. The Downs effort was found by raising the East Anglian effort in shots by the Downs/East Anglian catch ratio. Figure 11A shows the relation of stock density on fishing effort for the Downs spawning group for the period 1925–60. For a range of two times in fishing effort there is a halving of stock; the regression is significantly different from zero ($p < 0{\cdot}01$). If the efficiency factor were taken into account, it would be seen that the stock had been much further reduced.

For the Buchan and Dogger spawning groups the estimate of effort used was derived from that given by Parrish and Craig (1963). They tabulated the German Fladen catch and the German Fladen fishing effort, adjusted for changes in power and efficiency from Lundbeck (1959). Then the German Fladen effort was raised by the ratio of the total catch to the German Fladen catch. The proportions of the Buchan spawners in the mixed fisheries to give the total catch were taken by me to be: Buchan 40% (1930–50), 53% (1951–60); Fladen, 48% (1955–60); Shetland, 28% (1930–50), 72% (1951–60); Viking, 66%. Figure 11B shows the relationship of Buchan stock on effort. An increase of about three times is shown between the mean for the period 1930–53 and the peak in 1955 and 1956. A negative but non-significant line fits the data from 1954–60.

The same technique was used for the October Dogger stock from 1949–60. The proportions of the Dogger spawners in the mixed fisheries were taken to be: Shetland, 12%; Buchan, 50%; Viking, 33%; Fladen, 37% (1949–54), 28% (1955–60); Dogger, 70% (1949, 1950), 50% (1951–60). The results are given in Figure 11C; a negative but non-significant line fits the data from 1949 to 1960.

From the results given in Figure 11, the following conclusion may be drawn: that the effect of fishing is clearly shown for the Downs spawning group, but not for the Buchan and Dogger spawning

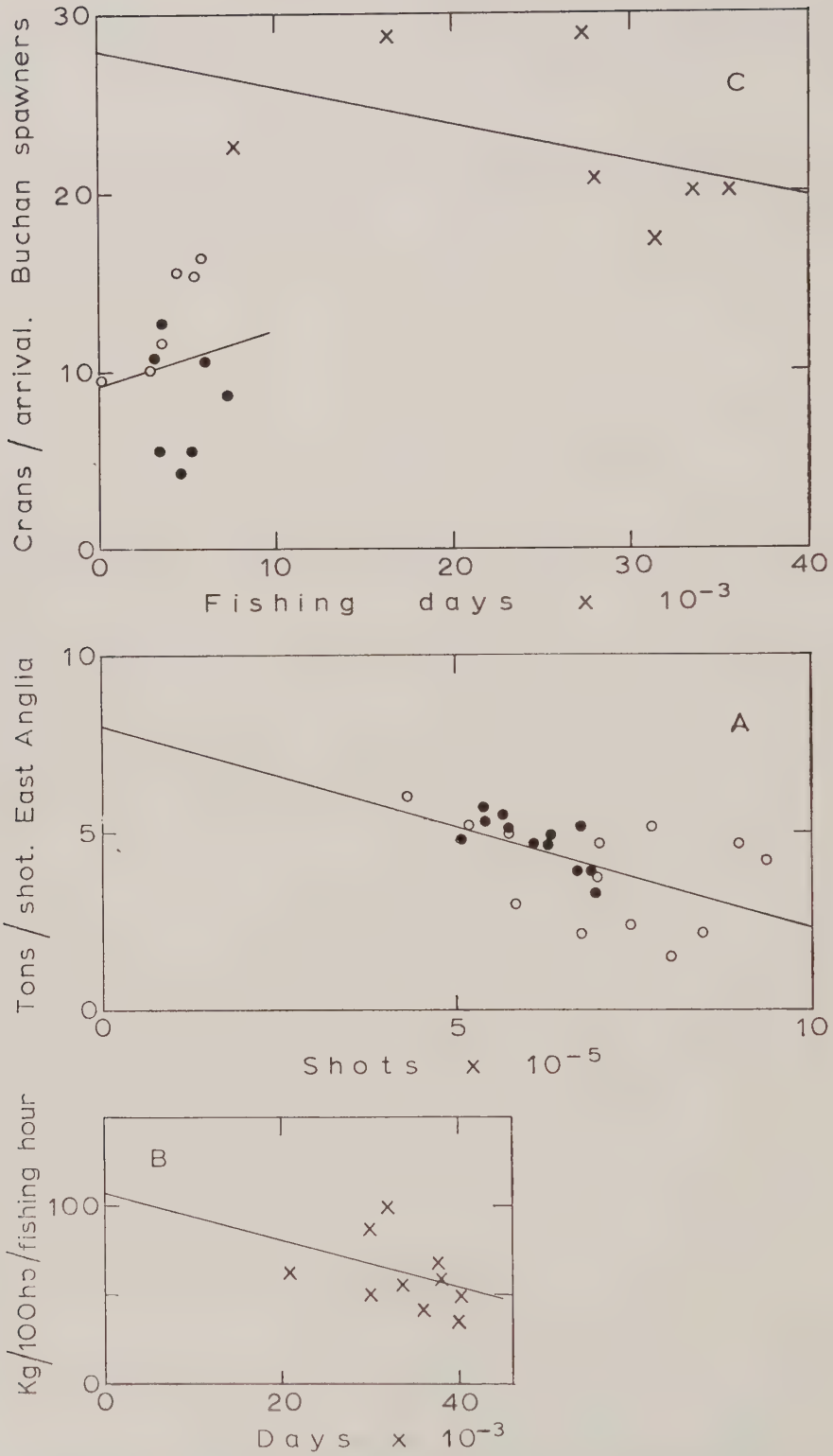

Fig. 11. *Relation of catch per effort on effort for each of the three spawning groups in the North Sea. For the method of estimating the three sets of data, see text. Solid circles represent the pre-war data and open circles the post-war data. Crosses represent the post-recruitment change data in the Buchan spawning fishery.*

groups. It is possible that a similar relationship might emerge for the two Bank groups in later years, in view of the increase in effort in the northern North Sea in recent years (Herring Assessment Group Report, 1964).

The results obtained in this section are in agreement with the general biological picture that has emerged in the North Sea – that the reduction in stock observed in the southern North Sea has not been so marked in the north, year-classes surviving for a shorter period at East Anglia than in the Buchan fishery.

If the efficiency change shown in Figure 5 were to be taken into account a much sharper regression of stock density on effort is shown. But as Cushing and Bridger show, in Part III, recruitment to the Downs stock has declined during the period. It happens that the increase in efficiency is of the same magnitude, inversely, as the decline in recruitment. Further, if the efficiency change is really one of a nature common to all three spawning groups, the relative states of the three stocks are shown adequately in Figure 11.

CONCLUSION

In this section three separate lines of evidence are considered. Independent estimates of natural mortality in the Downs stock and in other autumn-spawning herring stocks, combined with independent estimates of fishing mortality in the Downs stock, show that $M = 0{\cdot}20$–$0{\cdot}25$ and that $F = 0{\cdot}70$–$0{\cdot}80$. A separation of fishing and natural mortality in the correlation of total mortality on effort for the Downs stock yields an estimate of $M = 0{\cdot}09$. Regressions of stock density on effort for all three spawning groups were calculated, but only that for the Downs stock is significantly different from zero.

For the Downs stock, fishing mortality is probably three times the natural mortality and hence the effect of fishing can be clearly seen. For the Buchan and Dogger stocks it is likely that fishing mortality is about twice as great as natural mortality.

4. THE EFFECT OF GROWTH ON THE YIELD CURVE OF THE HERRING

Since 1930 the herring in the North Sea have been growing more quickly. Not only has the length for age of herring increased sharply, particularly during the fifties (Burd and Cushing, 1962), but the values of W_∞ have increased. To examine this point a little more critically, yield curves have been calculated for five year-classes, 1932, 1943, 1947, 1950 and 1953. Table 12 gives all the parameters used:

Table 12. *Parameters of yield equations based on five year-classes*

Year-class	1932	1943	1947	1950	1953
t_λ (years)	10·0	10·0	10·0	10·0	10·0
M	0·20	0·20	0·20	0·20	0·20
$t_{\rho'}$ (years)	3·0	3·0	3·0	3·0	3·0
t_0 (years)	−1·76	−2·24	−1·22	−0·79	−0·188
K	0·35	0·31	0·40	0·46	0·57
W_∞ (g)	196	215·9	224	224	198

The equation used was

$$\frac{Y_w}{R'} = FW_\infty \sum_{n=0}^{n-3} \frac{\Omega_n \, e^{-nk\,(t_{\rho'} - t_0)}}{Z + nk} [1 - e^{-(Z+nk)(t_\lambda - t_{\rho'})}]$$

where Y_w is the yield in g;

where R' is the number of recruits;

where F is the instantaneous coefficient of fishing mortality;

where W_∞ is the asymptotic weight of herring in g;

where t_0 is the age at zero weight, calculated from the Bertalanffy growth equation (which may be positive or negative);

where $t_{\rho'}$ is the age at which fish enter the exploited phase;

where t_λ is the age of the fish at the end of the lifespan;

where Z is the instantaneous coefficient of total mortality;

where M is the instantaneous coefficient of natural mortality;

where K is the relative rate at which the annual growth increments decrease.

(Beverton and Holt, 1957)

Figure 12 shows A: the calculated yield curves and B: theoretical stock density curves for each of the five year-classes. There are two conclusions to be drawn from this figure:

1. When $F > 0{\cdot}5$, any increase in effort will only lead to small increases in total catch. A doubling of fishing effort will only increase the total catch by a few per cent.
2. The difference in yield per recruit between the 1932 and 1950 year-classes, due to growth alone, is of the order of 20% when $F > 0{\cdot}5$. As growth has increased since the thirties, in much the same way as fishing effort has, much of the effect of fishing has been masked. Let us suppose that F has increased from 0·25–0·30 to 0·50–0·60 in the period 1930–60. Then Y_w/R' would increase for the 1932 year-class from 75g to 95g. At F 0·50–0·60, the increase in yield per recruit due to the growth change between the 1932 year-class and the 1950 year-class is from 95g to 120g, which is the same percentage increase as that due to the increase in F. So between the thirties and the fifties, yield has increased by 40%, and half of this increase is due to fishing and half to increased growth.

It can be shown that the catches and catches/effort of the five year-classes were correlated with the expected values of Y_w/R' or $Y_w/R'F$. Y_w/R' was estimated for an estimated value of F during the period of three years during which the year-class was abundant in the fishery. The real importance of this section is to show that during the thirties and the fifties the effect of increased fishing has been masked by the increase in weight for age of fish. Indeed the increase in weight of catch due to the doubling of fishing effort is possibly of the same order as the increase in weight of catch due to the growth change. This fact, fortunate for the fishermen, has added to the difficulties of the fisheries biologists.

5. THE REGULATION OF CATCH PER UNIT OF EFFORT

It is obvious from the yield curves (Figure 12A) that regulation to obtain the maximum sustainable yield is impracticable. Cushing (1959) suggested that regulation by catch per unit of effort was possible. There is a low level of catch/effort at which fishing stops. The state is shown in Figure 13,

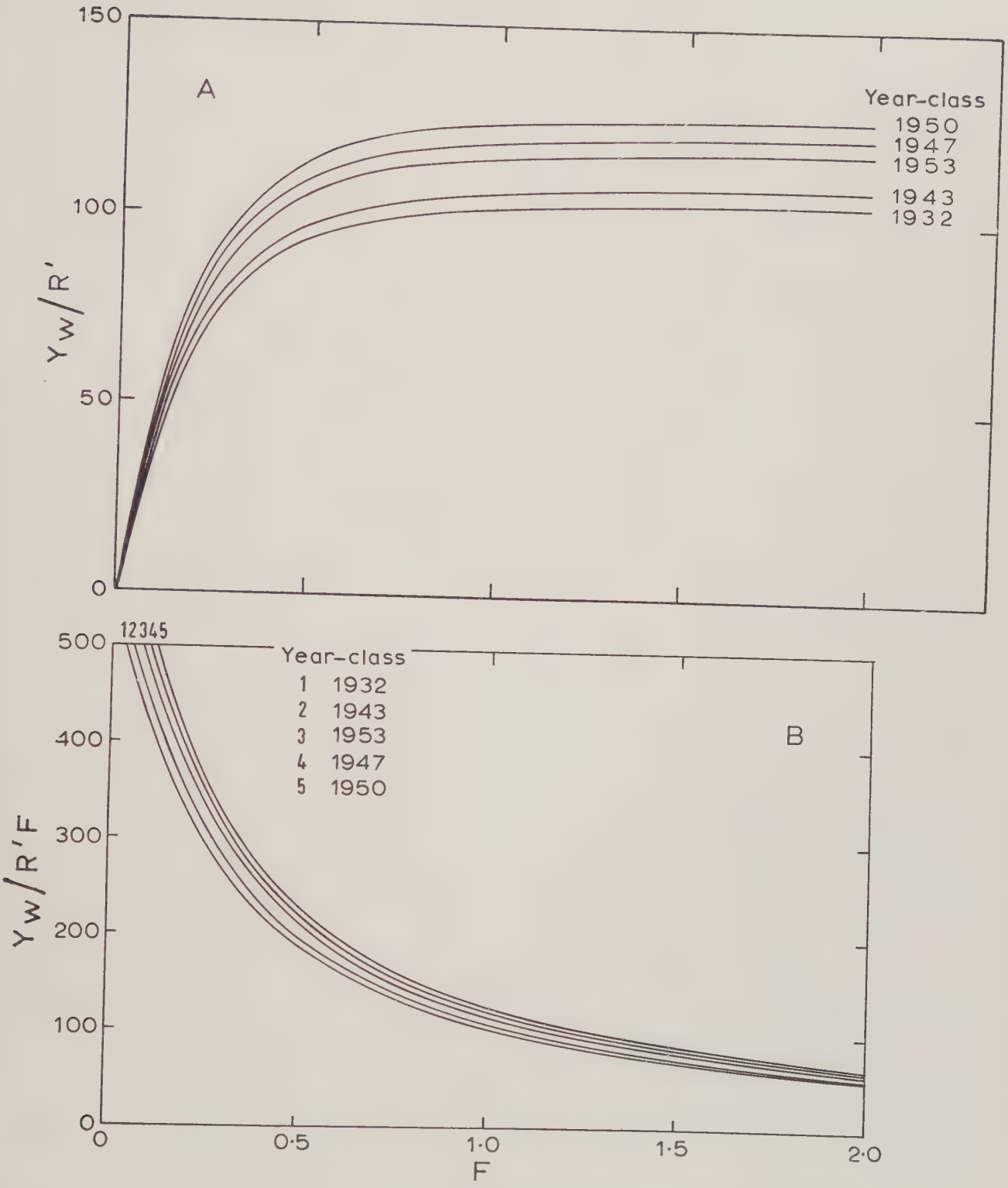

Fig. 12. A. *Yield curves calculated for five year-classes.*
B. *Curves of* Yw/R′F *on* F *for the five year-classes.*

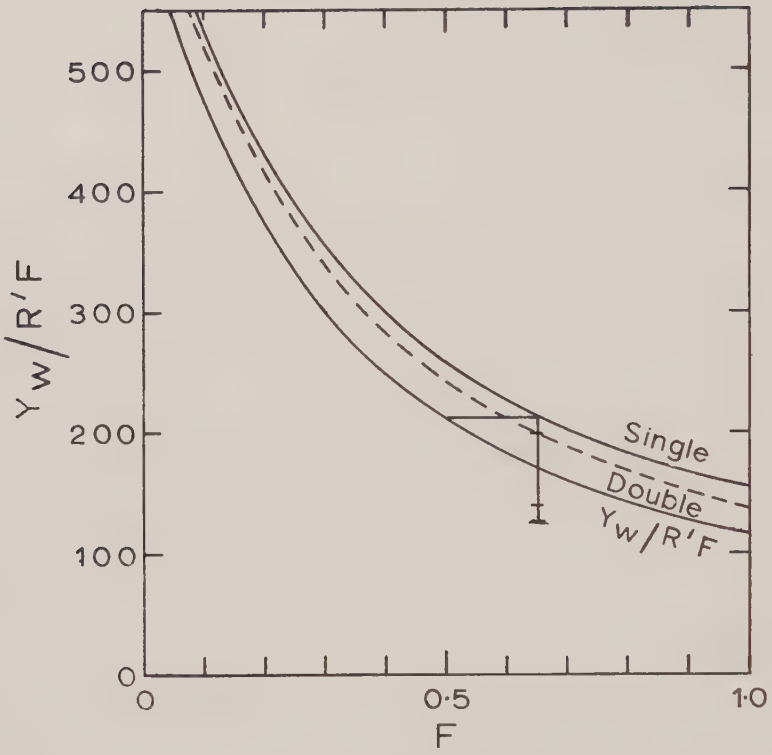

Fig. 13. *The variability of the catch per effort due to recruitment variation under conditions of single and partial recruitment. The curve* Yw/R′F *is shown for different values of* F. *The other two lines show the variability in* Yw/R′F *expected under conditions of single recruitment, or double recruitment (half at three and half at four years of age). The reduction in* F *needed to prevent economic failure of the fishery is shown at* F = 0·65.

which gives the variability in $Y_w/R'F$ due to recruitment, at $F = 0{\cdot}65$. The variability in $Y_w/R'F$ is shown separately for single recruitment and for recruitment partially at three and partially at four years of age ('double' recruitment). A reduction in F to 0·5 would ensure that the low level of catch/effort (at $F = 0{\cdot}65$) would not be reached merely by changes in recruitment. The decision to stop fishing seasonally or locally is destructive to a complex and seasonal trade like the herring trade. It is arguable that the stocks recover naturally, but the real effect is that the specialist trades become replaced by more industrial outlets. The decision to accept regulation is really an economic one: is the sacrifice of a little total catch worth the gain of an appreciably higher and more stable catch per unit of effort?

In order to arrange the facts to help reach a decision, Figure 14 has been constructed. Three parameters are shown; for a range of values of fishing mortality are given the percentage reduction in F needed at the low level of stock to yield a percentage gain in catch per effort as consequence and a percentage loss in total yield as consequence. Each calculation was made from the yield curves and the catch/effort curves in Figure 12. For example at $F = 0{\cdot}6$ (Fig. 14B) a reduction in F of 25% is needed (to $F = 0{\cdot}45$) in order to damp the variability due to recruitment. The result would be a gain in catch per effort of 22% and a loss of 5% in total yield. Given that the lower level of F can be agreed and estimated, the consequences in value in catch per effort or in yield can be calculated for any reduction in F.

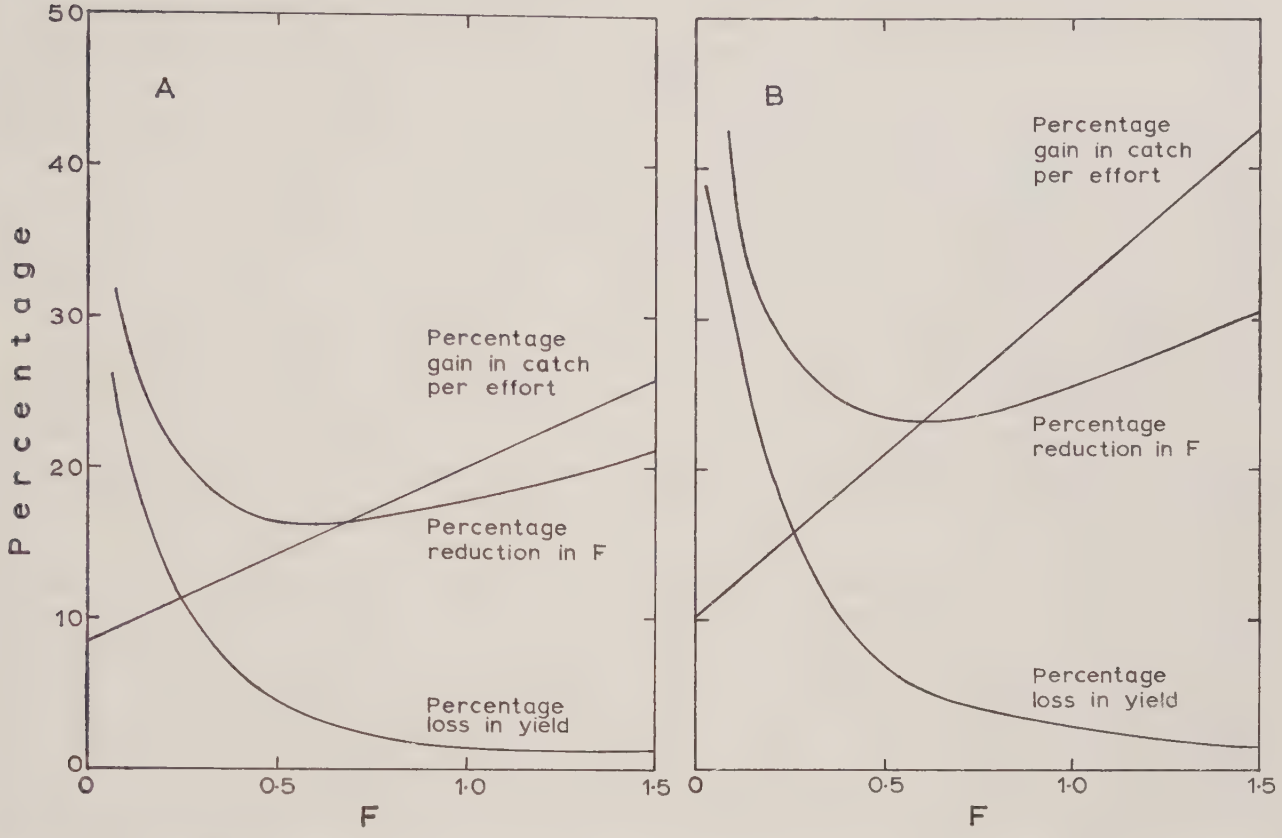

Fig. 14. *The percentage reduction in* F *needed to prevent economic failure of the fishery is shown at all values of* F. *The consequent percentage gain in catch per effort, and the percentage loss in yield, are also shown.*
A. *With double recruitment, half at three years of age and half at four years of age;*
B. *With single recruitment, wholly at three years of age.*

6. DISCUSSION

THE analysis of the effect of fishing on the North Sea autumn-spawned herring has taken the course of a long and complex argument. The reason is that three groups of adult fish segregate to their spawning grounds and mix on the feeding grounds. It is impossible as yet to give these groups the status of race, which implies a separate coherence between generations. This is because the possible segregation of the groups is not understood in the recruitment mechanisms. However the word 'stock' can be applied to such adult groups that appear to retain their identity in year-classes from year to year (Cushing, Part I).

Given the mixing rate (see Appendix 2) the proportion of effort exerted on the Downs stock in the North Sea can be readily calculated. It was shown, however, that a change in fishing efficiency had taken place. This was shown in a time series of the ratio of catch per shot to stock.

It was shown that mortality rates, as estimated in the East Anglian fishery, were biased by changes in mean length. As the mean length of the fish increased so mortality rates were biased downwards. It is likely that this effect was a consequence of the fleets' mesh retention curve which affects the sampling of the older fish only (Burd, 1963). A statistical adjustment was made by which the effect of the bias has been minimized.

The relation between mortality and effort and the relation between stock and fishing effort both show clearly that the dominant cause of mortality in the Downs stock has been that due to fishing.

F/Z might be as high as 0·6 or 0·8, with Z at 0·80 or 1·0. Relations between stock density and fishing effort have been examined for the three spawning groups. Only that for the Downs stock is significantly different from zero; for the Buchan and Dogger stocks, negative regressions were found. This confirms the general impression that the abundance of the Downs stock has been substantially affected by fishing but that the Buchan stock has been only recently affected; it is only since 1955 that the Buchan stock has been comparable in size to the other two (ICES, 1965).

The form of regulation was discussed, together with the nature of the yield curves. It was shown that the effect of fishing on the yield, and to a less extent on the catch per effort, had been masked by the growth change which had taken place at the same time as the effort change.

It is the complexity of the problem that has delayed solution for so long. The pre-war herring workers had evidence of racial separation between spawning groups (Wood, 1936; Schnakenbeck, 1931; Buchanan-Wollaston, 1933) and at the same time possible evidence was available that recruits to a given stock originated from all three spawning groups (Hodgson, 1929). The solution to this dilemma was to establish the identity of the adult fish as spawning groups, as shown by Burd (Burd and Cushing, 1962) and to establish the homogeneity of vital parameters within the Downs stock, as shown in Part I.

Given that the three groups do segregate to their spawning grounds within their adult lives, the problem of their mixture on the feeding grounds becomes important. The solution given by Cushing (Part I) yields an average value based on long time series. No estimate of the rate of mixing in a particular year is at present possible. It is likely that the average rates are of the right order, because they have been derived by two independent methods. The difficulty here is to devise good methods of checking the result, when the Downs stock is well reduced, when tagged herring do not live long in the North Sea, and when other methods of 'racial' diagnosis are not sufficiently well advanced.

It has been shown that fishing on the Downs stock is the dominant cause of mortality; indeed if $M \doteq 0{\cdot}20$, F is now as high as 0·75. Total mortality on the Buchan stock is high, about 0·75 and that on the Dogger stock is as high as that on the Downs stock. There is no evidence that for these two stocks $M > 0{\cdot}20$. Hence fishing is also the dominant cause of mortality in the Buchan stock and Dogger stock. Thus we may justly say that fishing is the dominant cause of mortality in the North Sea autumn-spawning herring. From Figure 14B, with a reduction in fishing mortality of 23% (for $F = 0{\cdot}55$ in the Buchan stock or for $F = 0{\cdot}75$ in the other two stocks), catch per effort would increase by 23–27%, at the cost in total yield of 3–6%.

7. SUMMARY

A BIAS in the mortality rates of the East Anglian herring was found associated with changes in mean length. Presumably it is due to some selective effects of the drift net. It was also found that after the war the effort exerted by East Anglian driftermen became nearly three times as efficient as before the war. Catches in the whole North Sea were separated by the proportions of the three spawning groups in the different fisheries.

Natural mortality was estimated to be 0·2. Hence fishing mortality as $Z-M$ for the North Sea herring was high, perhaps 0·5 for the Buchan stock and 0·75 for the Downs stock. The relation between mortality and effort for the Downs stock suggests that F/Z is very high, about 0·75. Regressions of stock density on effort for each of the three North Sea stocks are given.

The effect of growth on yield was analysed. The increase in catch since the thirties was shown to be as much due to an increase in weight as to an increase in fishing. A short discussion of regulation by catch per unit of effort is given.

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APPENDIX 1

East Anglian Mortality Rates

	3/4	4/5	5/6	6/7	7/8	8/9	5–7	5–9
1924/5	—	—	0·37	0·39	1·16	0·11	0·38	1·03
1925/6	—	—	0·30	0·75	0·77	1·61	0·52	0·87
1926/7	—	—	0·38	0·83	1·00	2·30	0·60	1·14
1927/8	—	—	0·27	0·13	0·22	0·45	0·20	0·27
1928/9	—	—	0·0	0·14	0·19	0·69	0·07	0·26
1929/30	—	—	0·65	0·43	0·37	0·98	0·54	0·61
1930/1	—	—	1·07	0·62	0·63	0·49	0·84	0·70
1931/2	—	—	0·81	0·41	0·74	0·98	0·61	0·74
1932/3	—	—	0·32	0·59	0·13	0·64	0·45	0·42
1933/4	—	—	0·24	−0·08	0·47	0·34	0·08	0·24
1934/5	—	—	0·61	0·69	0·94	0·36	0·65	0·65
1935/6	—	—	−0·46	0·21	0·51	0·21	−0·22	0·12
1936/7	—	—	0·52	0·75	0·92	0·59	0·63	0·70
1937/8	—	—	0·71	0·95	−0·11	0·62	0·83	0·54
1946/7	—	0·33	0·63	0·18	0·90	0·89	0·40	0·65
1947/8	—	0·38	0·13	−0·39	0·46	0·11	−0·13	0·08
1948/9	—	0·28	0·45	0·59	1·64	1·48	0·52	1·04
1949/50	—	0·60	0·48	0·50	0·69	0·33	0·49	0·50
1950/1	—	0·31	0·53	0·57	0·48	0·62	0·55	0·55
1951/2	—	0·46	0·32	0·52	0·69	0·56	0·42	0·52
1952/3		0·83	1·06	1·12	1·04	0·80	1·09	1·01
1953/4		0·39	0·36	0·07	0·45	0·18	0·21	0·27
1954/5		1·38	1·09	1·13	1·22	1·44	1·11	1·22
1955/6	0·35	0·41	0·43	0·89	0·98	—	0·68	0·86
1956/7	1·12	1·68	1·74	1·85	1·95	—	1·81	1·81
1957/8	1·26	1·56	0·94	1·01	1·49	—	0·95	1·00
1958/9	0·88	0·98	0·85	0·98	0·92	—	0·93	0·77
1959/60	1·30	1·93	2·51	3·19			2·85	

APPENDIX 2

THE AVERAGE PROPORTIONS OF THE DOWNS STOCK IN THE MIXED FISHERIES IN THE NORTHERN AND CENTRAL NORTH SEA

A. *Proportions of Buchan spawners and Downs spawners (East Anglian fish) in the Northern North Sea in the* 1930*s*

Mixed fishery	Buchan spawners	Downs spawners
Buchan pre-spawning	40%	44%
Shetland	28%	—
Fladen	—	30%

B. *Proportions of October Dogger spawners and Downs spawners (East Anglian fish) in the general Dogger fishery*

	1930–50	1949–58
Downs spawners	29%	—
October Dogger spawners	—	36%

C. *Proportions of the three spawning groups, as recruits and as middle-aged fish, on the Fladen ground*

		1932–54	1955–9	1932–59
Downs	Recruits	24%	—	22%
	Middle-aged	26%	—	—
Buchan spawners	Recruits	—	48%	13%
	Middle-aged	—	—	—
October Dogger spawners	Recruits	—	—	—
	Middle-aged	37%	28%	

D. *Proportions of the three spawning groups on the Fladen ground*

	1950–4	1955–9
Downs spawners	50%	19%
Buchan spawners	—	48%
October Dogger spawners	37%	28%

APPENDIX 3

SOURCES OF DATA USED IN ESTIMATING THE CATCHES OF HERRING IN THE NORTH SEA

1. *Buchan fishery*	1924–56	Parrish, B. B. and Craig, R. E. (1957), *Rapp. et Proces-Verbaux du CIEM,* **143** (I).
	1956–7	*Ann. Biol. du CIEM.*
	1958	Statistical Newsletter of ICES on herring.
2. *Fladen fishery*		
(*a*) Aberdeen trawl	1924–37	Scottish catch from region IVa of the North Sea (*Bull. Statist. du CIEM*), less catches from Buchan and Shetland fisheries (Parrish, B. B. and Craig, R. E. 1957, *Rapp. et Proces-Verbaux du CIEM*, **143** (I).
	1946–57	*Ann. Biol. du CIEM.*
	1958	Statistical Newsletter of ICES on herring.
(*b*) German trawl	1924–57	*Jahresberichten der deutschen Fischereien.*
(*c*) German drift	1924–9	German catch (*Bull. Statist. du CIEM*) less German trawl catch. The portion on the Fladen ground was estimated.
	1930–52	Estimated from monthly catch figures in *Bull. Statist. du CIEM.*
	1953–7	*Jahresberichten der deutschen Fischereien.*
	1958	Statistical Newsletter of ICES on herring.
(*d*) Dutch drift	1924–58	Estimated from monthly catch figures in *Bull. Statist. du CIEM.*
(*e*) Dutch lugger	1955–8	Estimated from figures published in Statistical Newsletter of ICES on herring, charted.
(*f*) Dutch trawlers	1945–58	Monthly catches from *Bull. Statist. du CIEM* from May to September were apportioned to area by the percentage catch of German trawlers in each area.
(*g*) German cutters and mixed trips		*Jahresberichten der deutschen Fischereien.* Allocated to area in the same proportion as the German trawl catch, when the area was known. In 1954–7, there are quantities (18 000–30 000 tons) which cannot be accounted for.
(*h*) French	1924–39	Total North Sea catch from *Bull. Statist. du CIEM.*
	1946–58	Catches from area IVa and IVb from *Bull. Statist. du CIEM.*
		All years were apportioned to area by the percentage catch of German trawlers.
(*j*) *Belgium*	1945–58	As France.
(*k*) *Poland*		Pre-war total North Sea catch was assumed to be all from Fladen. Post-war catch is that from area IVa (*Bull. Statist. du CIEM*) less that from January to May. Since 1956 catches on Fladen have been taken from Statistical Newsletter of ICES.
(*l*) *Sweden*		Post-war catch from June to October from monthly catches in *Bull. Statist. du CIEM* I or from areas IVa and IVb if less.
3. *Gut and Dogger*		The same sources of data have been used for the Gut and Dogger as for Fladen, with the following exceptions. It will be seen that 'Gut and Dogger' is a loose term here embracing also all herring fisheries between the Gut and the English coast.
(*a*) *Poland*		Catches from area IVb in *Bull. Statist. du CIEM.*
(*b*) *England*		Total North Sea catch less catches in Southern Bight and Channel.
4. *Southern Bight*		
(*a*) German trawl	1948–57	*Jahresberichten der deutschen Fischereien.*
(*b*) Dutch trawl	1924–57	*Bull. Statist. du CIEM*, monthly tables (Oct.–Dec.) or *Ann. Biol. du CIEM.*
(*c*) French	1924–37	*Bull. Statist. du CIEM* (Channel only).
	1946–57	*Bull. Statist. du CIEM* (Areas IVc and Channel).
		(In 1950 and 1951, IVc was estimated as a proportion of IVa, b, c, using the average percentage distribution, 1957–9.)
(*d*) Poland	1955–7	*Bull. Statist. du CIEM* (Areas IVc and Channel). Statistical Newsletter of ICES.
(*e*) Belgium	1924–37	*Bull. Statist. du CIEM.* (Total North Sea.)
	1946–56	Gilis, Ch. (1957) *Rapp. et Proces-Verbaux du CIEM* **143** (I).
	1957–8	Statistical Newsletter of ICES.

(*f*) German drift (and lugger trawl)	1924–9	As Fladen.
	1930–7	Estimated from monthly catch figures of *Bull. Statist. du CIEM*.
	1946–9	Estimated from total catch figures.
	1950–2	Binnensee and Kanal catches estimated as a proportion of catch in Oct.–Dec., in Oct.–Dec. in *Jahresberichten*. Binnensee and Kanal catches/Total catches, Oct.–Dec. (1953–6 = 0·66).
	1953–7	*Jahresberichten der deutschen Fischereien* (Binnensee and Kanal).
	1958	Statistical Newsletter of ICES.
(*g*) Dutch drift	1924–37	Catches in Oct.–Dec. from monthly figures in *Bull. Statist. du CIEM*.
	1946–60	Catches in Oct.–Dec. (*Bull. Statist. du CIEM*) reduced in proportion to Shots south of 53°N (Oct.–Dec.)/Total shots: from de Veen et al., *Ann. Biol. du CIEM*.
(*h*) Dutch lugger	1946–57	Catches in Oct.–Dec. (*Bull. Statist. du CIEM* and *Ann. Biol. du CIEM*), reduced as drift.
(*j*) England		Effort figures from Hunder Bank and Cap Gris Nez and Silver Pit are excluded from the estimates of East Anglian effort; catches from these regions are included as a 'Southern Bight' catch, distinct from an East Anglian catch.

NOTE: ICES is the International Council for the Exploration of the Sea.
CIEM is le Conseil International pour l'Exploration de la Mer, which is, of course, the same body.

APPENDIX 4

Catches of herring in the North Sea from various named fisheries (collected as in Appendix 3) and split for the Downs stock by the proportions given in Appendix 2; relevant catches for Dogger and Buchan stocks are tabulated but not split

	Dogger	D*	Fladen	D*	Buchan	D*	Southern Bight		East Anglian catch	East Anglian shots	Viking Bank	Shetland
1925	69 684	20 905	36 307	10 711	45 100	19 799	212 600	+ 3 546	155 000	35 049		
1926	98 058	29 417	41 227	12 162	71 250	31 279	189 300	+ 1 660	130 000	23 430		
1927	93 454	28 036	41 287	12 180	72 000	31 608	207 600	− 8 030	133 000	26 426		
1928	111 795	33 539	49 108	14 487	70 900	31 125	239 000	+ 2 246	165 000	27 629		
1929	112 946	33 884	82 123	24 226	80 400	35 296	280 700	− 32 767	170 000	29 298		
1930	92 435	27 731	69 725	20 569	63 500	27 877	254 500	+22 381	168 000	32 223		40 608
1931	137 393	41 218	68 196	20 118	32 350	14 202	207 150	−10 945	116 000	29 015		19 054
1932	100 980	30 294	77 572	22 884	40 291	17 688	165 800	+11 627	87 000	25 626		23 099
1933	128 627	38 588	90 463	26 687	38 237	16 787	192 350	− 7 856	90 000	22 262		11 769
1934	157 026	47 108	77 945	22 994	43 364	19 037	186 500	+ 1 901	80 000	17 180		26 865
1935	150 011	45 003	90 389	26 665	54 146	23 770	195 600	+ 1 701	105 000	19 846		35 692
1936	175 047	52 514	113 084	33 360	46 019	20 202	222 600	− 2 624	108 000	21 892		30 011
1937	228 998	68 699	136 943	40 398	34 455	15 126	252 100	+ 3 660	127 000	23 147		25 232
1947	214 401	64 320	133 699	39 441	53 201	23 355	154 450	+ 6 190	77 392	10 286	6 724	19 178
1948	168 014	50 404	131 298	38 733	51 728	22 709	223 900	−61 357	90 735	12 349	9 048	25 114
1949	178 820	53 646	144 385	42 594	25 073	11 007	165 100	+28 244	59 092	8 043	11 773	13 008
1950	181 292	54 388	119 422	35 229	19 309	8 476	171 600	+ 6 727	65 955	9 171	5 156	9 335
1951	266 012	133 006	148 849	73 829	29 055	7 815	233 300	−67 687	60 236	9 062	9 610	5 510
1952	203 129	101 565	129 000	63 984	54 655	10 767	218 800	+17 276	49 371	7 376	15 905	8 620
1953	224 606	112 303	145 943	72 388	62 437	7 243	263 300	−54 069	50 705	8 281	19 714	2 745
1954	218 434	109 217	122 521	60 770	43 619	3 010	203 100	+73 833	48 799	6 451	14 916	4 102
1955	170 339	85 170	232 320	43 212	47 910	2 396	142 600	+ 702	21 700	5 785	20 734	7 562
1956	163 909	81 955	161 407	30 022	25 727	1 286	115 600	+27 943	221 300	4 494	41 416	7 352
1957	150 661	75 331	179 254	33 341	22 873	1 144	116 400	+ 2 734	21 150	5 013	48 492	6 891
1958	156 101	78 050	143 657	26 720	14 005	691	80 076	+15 875	10 498	3 460	47 941	7 016
1959	147 098	73 549	220 474	41 008	31 968	1 898	68 456	−10 717	8 443	3 202	50 366	7 135
1960	135 464	67 732	137 852	25 640	16 677	834	47 218	+31 293	6 636	2 083	48 176	5 506

* Downs proportion.

NOTES TO APPENDIX TABLE 4

1. 'Dogger' includes all fisheries by all countries within the general Dogger area. It is a term more extensive than 'October Dogger Spawners' (see Cushing, in press).
2. 'Fladen' includes all fisheries by all countries within an area probably more extensive than the Fladen ground.
3. 'Buchan' and 'Shetland' comprise Scottish catches only.
4. 'Viking Bank' includes catches by all countries excluding Sweden (i.e. Germany, Holland, Scotland, Poland, USSR).
5. The Southern Bight catch is that reported by all countries in the calendar year. The second column is the quantity to be added or subtracted to obtain the catch from October/November to October/November in the year following the East Anglian fishery. This serves to correlate effort with mortality in the second year of the mortality pair.

PART III

The decline in recruitment to the Downs herring stock

D. H. Cushing and J. P. Bridger

INTRODUCTION

Bridger (1961) showed that, since 1946, estimates of larval abundance in the Downs stock of autumn-spawned herring have fallen about three times more quickly than have the estimates of stock density. Cushing (in Part II of this work) has found that an efficiency change of about the same order occurred in the post-war period amongst East Anglian drifters. The efficiency change was estimated as the ratio of catch per shot in numbers to stock in numbers. This is an exact estimate of q, the catchability coefficient, if mortality remains constant. During the period of change, mortality increased from 0·5 to 1·0 and the efficiency factor is biased upwards by 10% throughout the whole post-war period, as described in Part II. Similarly, because mortality rates are based on the ratio of stock densities in pairs of years, they are biased upwards by 7% (the annual increase in efficiency in the post-war period) which reduces the first bias slightly. Figure 1 shows the ratio of catch per shot in numbers to stock in numbers, in a time series from 1925 to 1960. These estimates have not been corrected for the small bias.

When the figures of total recruitment (in numbers/shot, as at three years of age) to the Downs stock are corrected by the efficiency factors derived from Figure 1, a post-war decline is noticed (Figure 2).

THE DECLINE IN RECRUITMENT

The decline in recruitment can be confirmed by making stock estimates at two separate periods. For example, the stock can be compared in two periods, 1930–7 and 1955–60. It will be recalled that the estimate of mortality is biased upwards in the later period by about 7% by the efficiency

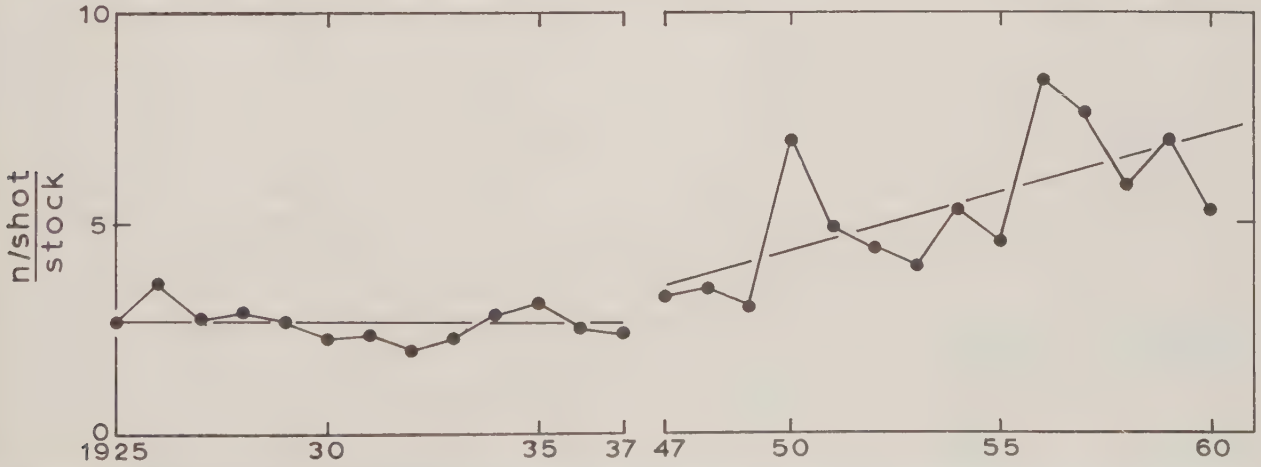

Fig. 1. *The change in efficiency in the East Anglian drift-net fishery. The index of efficiency (in the time series) is the ratio of catch/shot to stock (in numbers).*

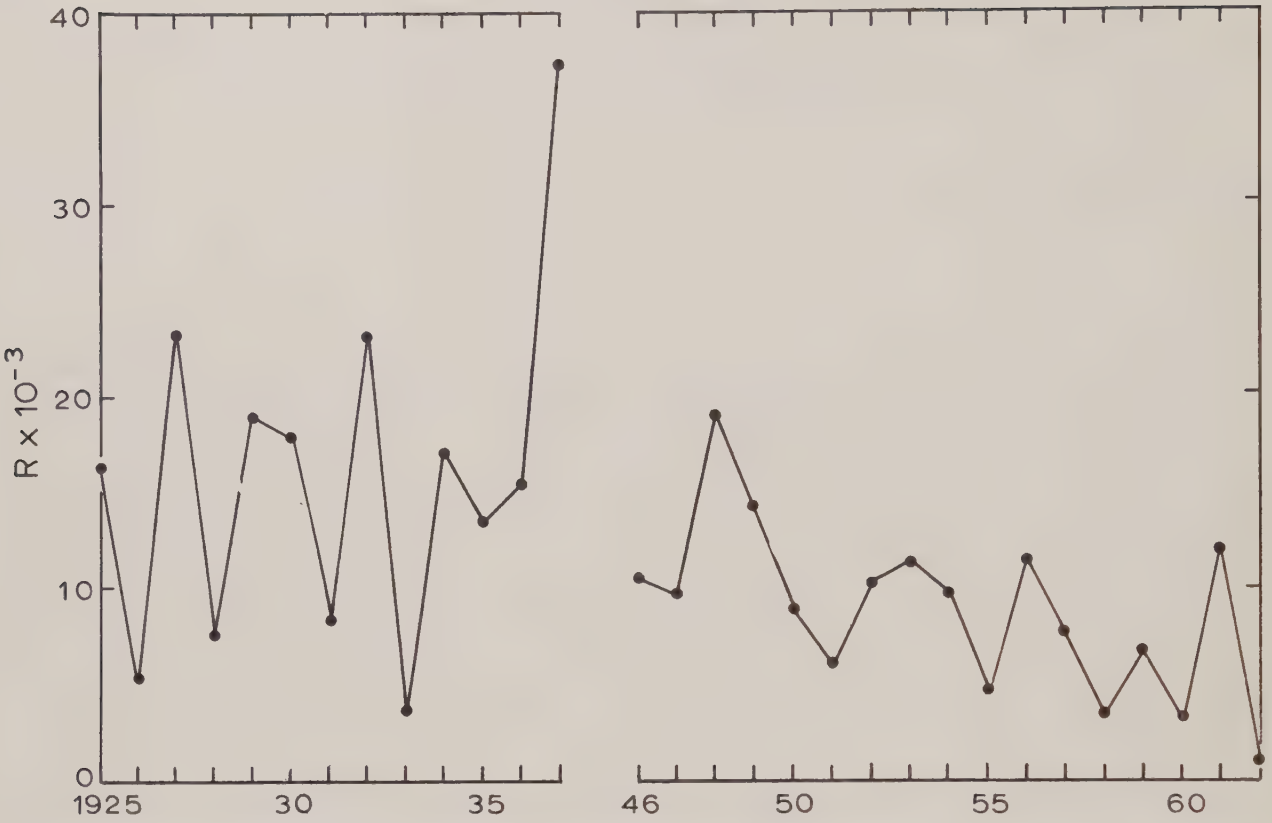

Fig. 2. *The decline in recruitment to the East Anglian fishery. The figures for total recruitment (as at three years of age, as estimated by Cushing, in Part II) are corrected by the efficiency factor derived from Figure* 1.

change described above. This is a small quantity compared with the changes about to be described, of 200–300%. In the estimation of stock, the following parameters were used (from Appendix Table 2, Part II and from Table 12 in Part II):

	1930–7	1955–60
Downs catches (tons)	301 995	217 976
Southern Bight catches (tons)	209 575	103 458
Z	0·50	1·00
F	0·25	0·75
K	0·35	0·46
W_∞ (g)	197	224
$t_{p'}$ (yrs)	3	3
M	0·25	0·25

Let ${}_1Y_w$ and ${}_1R'$ be estimates for the period 1930–7;

Let ${}_2Y_w$ and ${}_2R'$ be estimates for the period 1955–60.

Then ${}_1Y_w = 51{\cdot}8\ {}_1R'$, and ${}_2Y_w = 97{\cdot}1\ {}_2R'$;

$\therefore\ {}_1R'/{}_2R' = 1{\cdot}87 \times {}_1Y_w/{}_2Y_w$, or $1{\cdot}87 \times 301\,995/217\,976 = 2{\cdot}60$ (using Downs catches).

Downs catches include catches of the Downs stock in the northern and central North Sea as well as those in the Southern Bight (Cushing, in Part I). The method used of separating Downs catches

from those of other stocks in the northern and central North Sea is rather complex, so the Southern Bight catches are used in this paper to represent an unequivocal minimum catch of the Downs stock. Using Southern Bight catches rather than Downs catches, ${}_1R'/{}_2R' = 3{\cdot}50$. It is likely that ${}_1t_{\rho'} = 3{\cdot}5$, partial recruitment persisting until 1950–2; with ${}_2t_{\rho'} = 3{\cdot}0$, and ${}_1t_{\rho'} = 3{\cdot}5$, ${}_1R'/{}_2R'$ (Downs catches) $= 2{\cdot}35$, and ${}_1R'/{}_2R'$ (Southern Bight catches) $= 3{\cdot}16$. Between the two periods, K has increased from 0·35 to 0·46. Let us suppose that M increased in the same proportion; then the ratio of the recruitments in the two periods would have become reduced. The likely reduction in recruitment between 1930–7 and 1955–60 is of the order of 2·5, using Downs catches.

From Figure 2, the decline in recruitment in stock density using the efficiency factor is of the order of two to two and a half times between the same two periods as used above. Comparing the period 1958–62 with the pre-war average, recruitment has fallen by three times. The trend in the decline of recruitment in stock can be investigated with the method of virtual populations (Fry, 1949; Paloheimo, 1958). Catches at each age (of the Downs catch, or of the Southern Bight catch) were summed throughout the life of the year-class in the fishery. An average value of total mortality was calculated for the years during which the catches were summed for the year-class. The natural mortality rate was taken to be 0·25. The summed catches should be raised by $Z/F\,(1 - e^{-Z\lambda})$ to give estimates of stock in a year-class; as $1 - e^{-Z\lambda} \simeq 1$, the simple fraction Z/F was used. The reduction in virtual population from the year-classes of 1922–9 to those of 1952–5 is about $\times 2{\cdot}5$; if Southern Bight catches only are used to calculate the virtual populations, the estimated decline in recruitment is of the order of about $\times 2{\cdot}5$ to $\times 3{\cdot}0$. The downward trend in virtual population in the post-war period, using Downs or Southern Bight catches, is shown in Figure 3. The figure shows a decline of the same order as that given in Figure 1, which is based on estimates of stock density corrected by efficiency factors. Thus changes in stock density are shown also as changes in stock.

It is worth trying to establish the date by which the decline in recruitment to the Downs stock became significant. In Figure 3 the mean of the pre-war series of eight year-classes is given. The standard error of the pre-war mean is marked on the post-war series on both Figure 3A (using Downs catches) and 3B (using Southern Bight catches). The post-war series is fitted by moving means of eights (the number of pre-war observations) and it will be seen that the post-war trend does not exceed the pre-war mean until the 1952 year-class appears, in Figure 3A, and until the 1950 year-class appears, in Figure 3B. This method was suggested by Mr J. A. Gulland.

The year-classes estimated from the Downs catches represent estimates of stock based on catches in the northern and central North Sea as well as in the Southern Bight, and those estimated from Southern Bight catches alone are a minimal estimate. It is important to notice that the estimated decline in recruitment is of the same order with either set of catches. Similarly, with either set of catches the recruitment has fallen significantly with the 1950 or the 1952 year-class. This suggests that the recruitment failure is associated with the change in the pattern of recruitment (and the growth change) that took place between 1950 and 1952 (Cushing and Burd, 1957; Burd, 1962; Cushing, 1962).

The main conclusion to this section is that recruitment to the Downs stock has declined considerably in the post-war period. In Part II, Cushing showed that fishing mortality was the dominant cause of mortality in the post-war period ($F/Z = 0{\cdot}75$); he pointed out that catches in the Southern Bight have declined since 1955, and indeed the estimated Downs catches have also declined by a considerable proportion. From the yield curve, given in Part II, it is shown that an increase in fishing effort should never, in practice, lead to a decline in catch. The decline in recruitment since 1955 explains the observed decline in catch, with a sustained high fishing mortality.

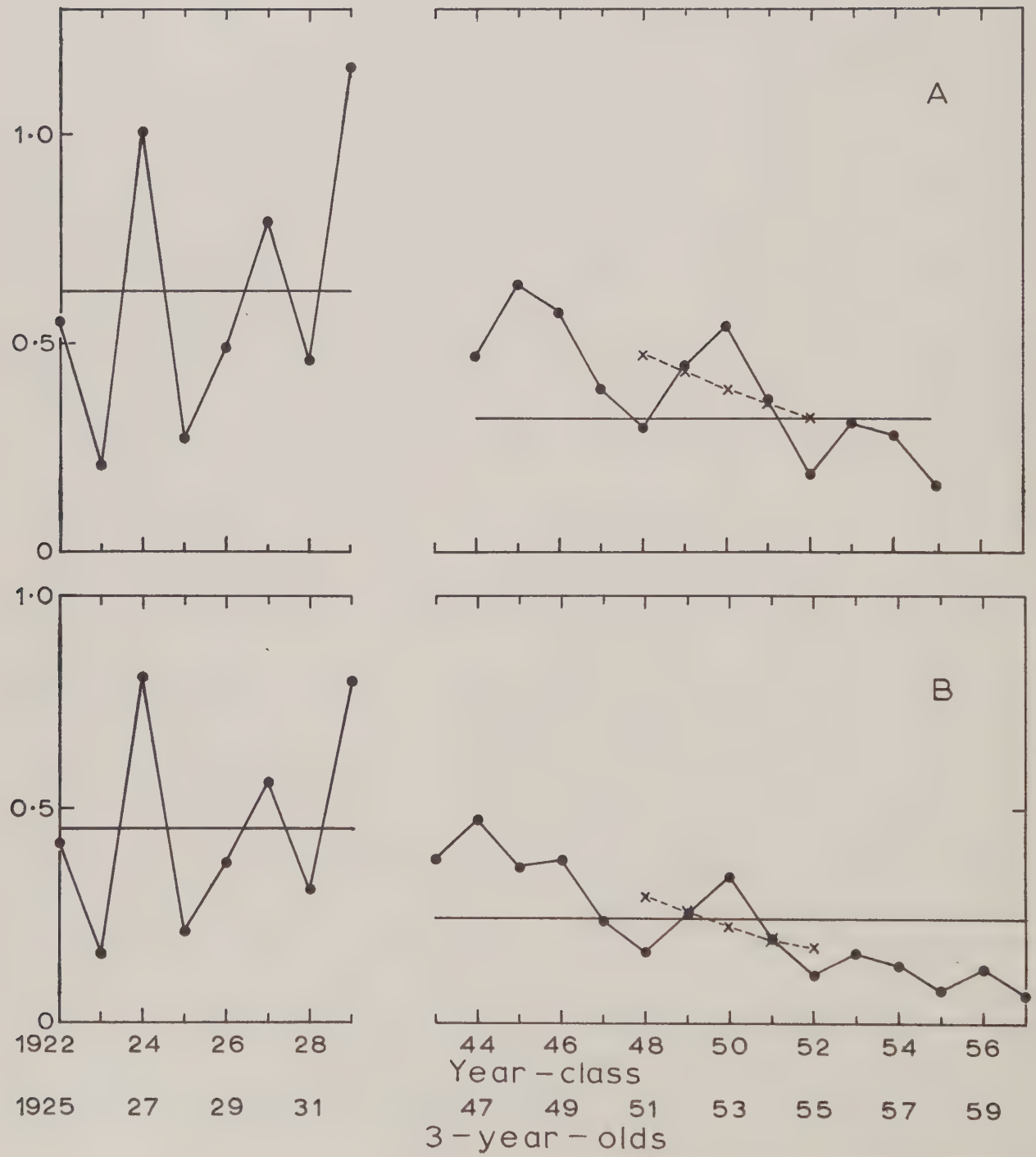

Fig. 3. *The decline in East Anglian recruitment as shown in virtual populations, using:* A. *Downs catches;* B. *Southern Bight catches. The mean of the pre-war set of observations is marked as a full horizontal line in the pre-war series; the standard error of the mean of the pre-war set is marked as a full horizontal line in the post-war series. The post-war series is fitted by moving means of eight (the numbers in the pre-war series), shown as a broken line.*

THE RELATION BETWEEN STOCK AND RECRUITMENT IN THE DOWNS STOCK

The relationship between stock and recruitment in the Downs stock of herring may be presented by using stock densities in numbers or by using estimates of stock in numbers. In the first method, the efficiency factor from Figure 1 is used. In the second it is not used, catches in any one year being raised by the fraction $Z/F(1 - e^{-Z})$, F and Z being the fishing mortality and total mortality respectively in that year.

Figure 4 shows the relation of recruitment to parent stock (as eggs/shot) or spawning power, both in stock densities (i.e., in numbers per unit effort corrected by the efficiency factor). Figure 4A shows the relation between recruitment and spawning power (stock density multiplied by fecundity, in age groups) of the parent stock aged 3–9. The regression of recruitment on parent stock is not significantly different from zero ($p = 0{\cdot}05$–$0{\cdot}10$). Figure 4B shows the relation between recruitment and spawning power of the parent stock aged 5–9. The reasons for restricting the adult stock to the older fish are given in a later section (below) where it is suggested that, effectively, the larvae of the younger fish are less viable. The regression of recruitment on parent stock (of fish of 5 + years of age) is significantly different from zero ($p = 0{\cdot}02$) and a curve is fitted to the data using the method of Beverton and Holt (1957), taking reciprocals of recruitment and of stock. It will be seen that the stock of older

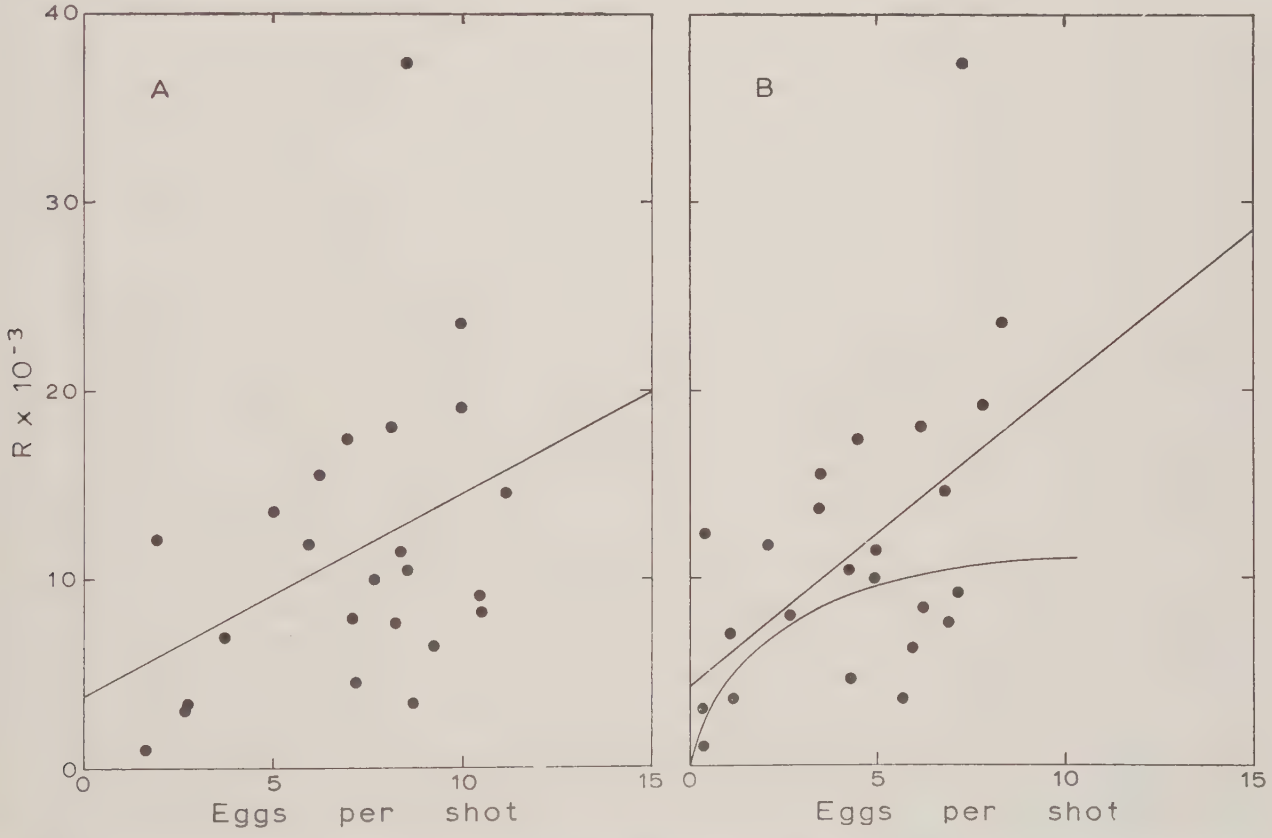

Fig. 4. *Relationship between stock (as eggs per shot) and recruitment in the Downs spawners, both in stock densities, by numbers.*
A. *All ages from three to nine; the regression of recruitment on stock is not significantly different from zero.*
B. *All ages from five to nine; the regression of recruitment on parent stock is significantly different from zero* (p — 0·02). *The curve is fitted by the method of Beverton and Holt* (1957).

fish (aged 5–9) has been reduced far enough for recruitment to have been reduced. The method of fitting depends on a significant relation between the reciprocals of recruitment and of stock. When the curve is transformed from reciprocals to fit the original data it does not pass through the mean. It could be fitted to the mean, but as the purpose is only to show the level of stock at which recruitment falls, this has not been done.

Figure 5 gives the relation between the log ratio of recruitment to stock (log R/S) and parent stock (S). If the ratio is considered as an index of survival, a negative regression shows that the survival rate is higher at low levels of stock and lower at high levels of stock. Such a regression would express the long asymptotic relation in stock between recruitment and parent stock, implying that recruitment is relatively constant about a wide range of stock. If it is assumed that recruitment is independent of stock for a wide range of stock values, then the relation in Figure 5 is a necessary, and perhaps artificial, consequence. If the assumption is not made, then the significant relation between log R/S and S suggests that recruitment is independent of stock. The regression in Figure 5 is significantly different from zero. A curve fitted with this line to the data is not an asymptotic one, but reaches a maximum. Such a curve is theoretically less acceptable than that of Beverton and Holt (1957), being an empirical one. But it can be used to fit a curve to data before recruitment falls. Whether it describes the stock/recruitment relation well over a range of data is unknown.

The second method uses estimates of stock in numbers rather than measures of stock density. Figure 6 shows the relationship between recruitment and parent stock, using Downs catches (Figure

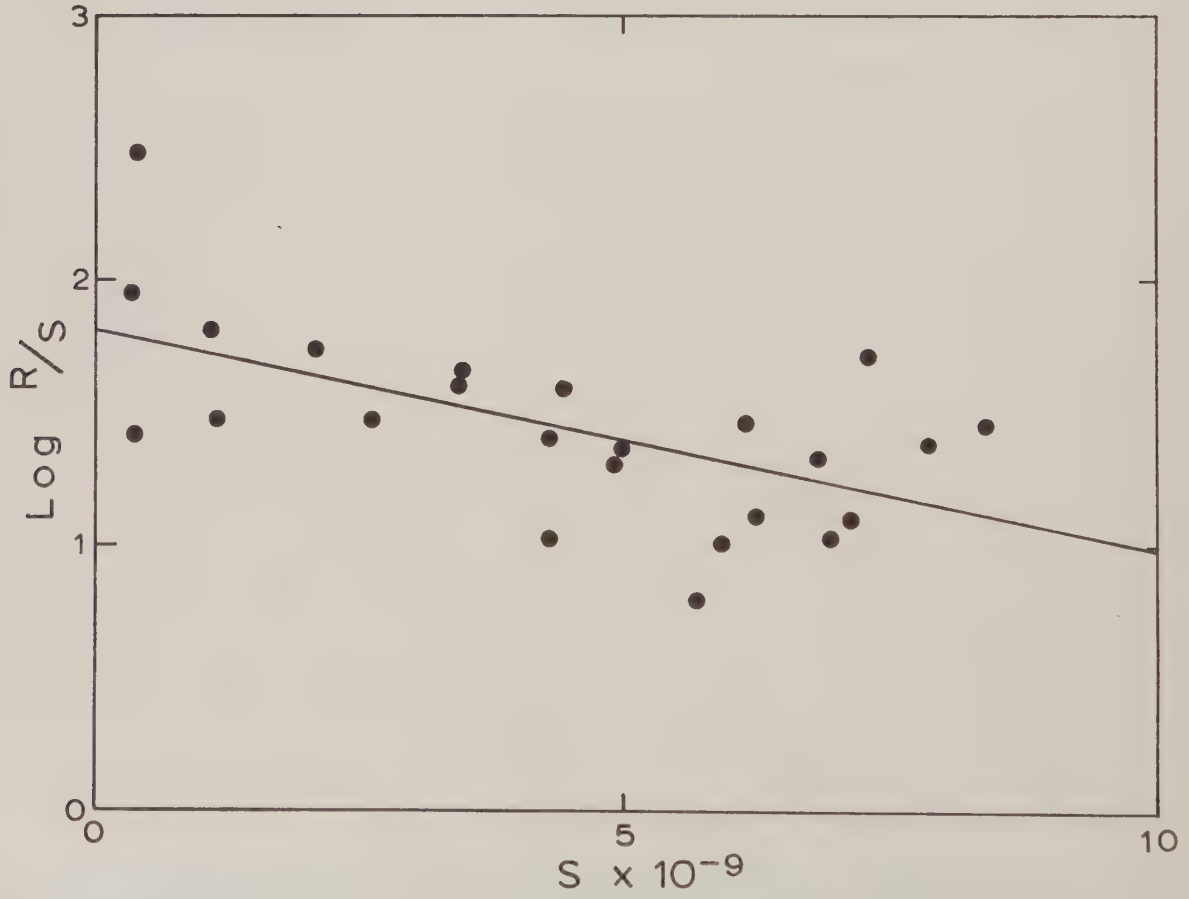

Fig. 5. *Relationship between the log ratio of recruitment to parent stock* (R/S) *and parent stock* (S), *derived from the data in Figure 4A. The negative regression is significantly different from zero.*

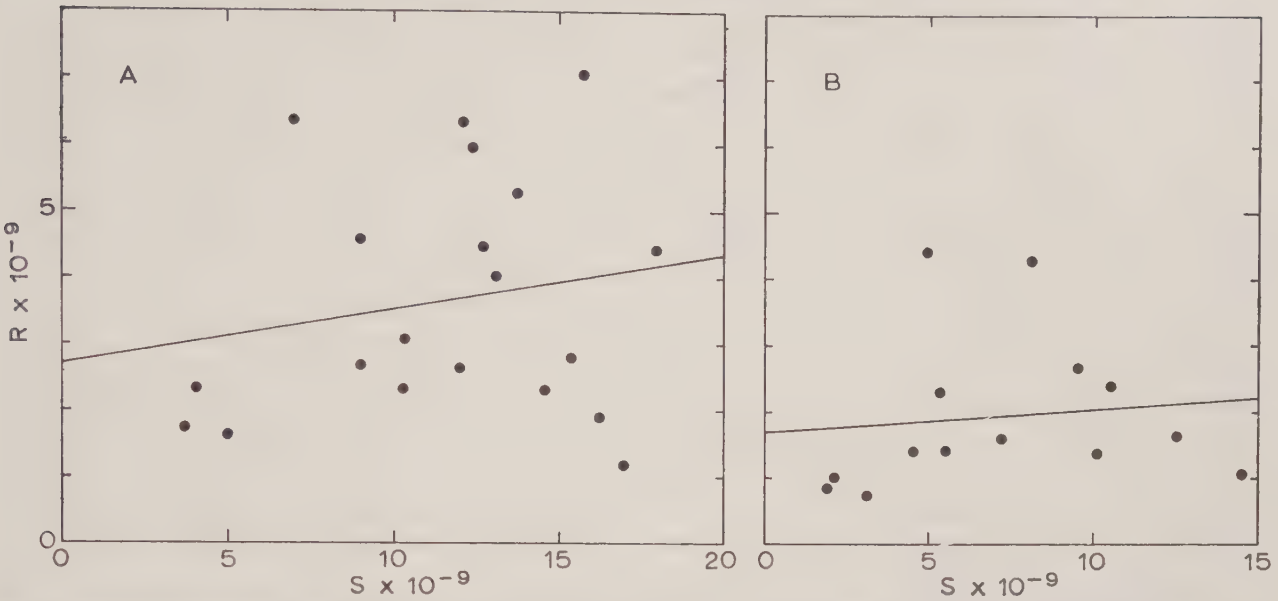

Fig. 6. *Relationship between stock and recruitment in the Downs spawners, using two different measures of stock. The correlations are not significantly different from zero, using:* A. *Downs catches;* B. *Southern Bight catches.*

6A) and Southern Bight catches (Figure 6B); neither correlation is significantly different from zero. Figure 7 shows the relation between the log ratio of recruitment to parent stock (log R/S) and the stock (S) for the two groups of catch; there are negative regressions in each set of data, indicating that the survival rate of recruits declines with increasing stock. There is a contrast between the results given in Figures 4 and 5 and those given in Figures 6 and 7. The stock density observations include the year-classes 1958, 1959 and 1960 in the years 1961, 1962 and 1963, necessarily absent from the estimates of stock[1]; these year-classes are very low both in stock and in recruitment, much lower than the last observations for the year-classes 1955, 1956 and 1957.

There is another way of examining the stock and recruitment relationship and that is by using the estimates of larval abundance. Figure 9 (below) shows a linear relationship between the stock densities of East Anglian spawners and the subsequent larval abundances. The larvae are predominantly in stage II, of 8–12 mm. in length, having fully survived the yolk-sac stage (Bridger, 1961). Consequently, the period between yolk-sac stage and the time of first feeding is not one in which density-dependent mortality is predominant. So if such mortality is to occur it must do so between the stage II larvae and recruitment to the adult fishery nearly three years later.

Figure 8 gives the relationship between recruitment and the resulting larval abundance. As there is a linear relation between stock density and larval abundance (as there is between stock and larval abundance, see Figure 10), the dependence of recruitment upon larval abundance is a justifiable form of the stock and recruitment relation. Figure 8A shows the dependence of recruitment, as stock density, upon larval abundance; to allow for partial recruitment, for the year-classes 1934, 1935, 1946 and 1947 recruitment was estimated as the sum of half the three-year-olds and half the four-year-olds in stock density. This procedure allows us to use the observations of the 1934 and 1935 year-classes, which cannot be used with measures of total recruitment. Figure 8B gives the dependence of recruitment, as virtual population, on larval abundance; in this figure, the estimates are based upon Downs catches (including the proportions caught in the northern and central North Sea) and upon Southern

[1] The stock estimates are derived from catches, the international record of which was only complete to 1960 at the time of writing.

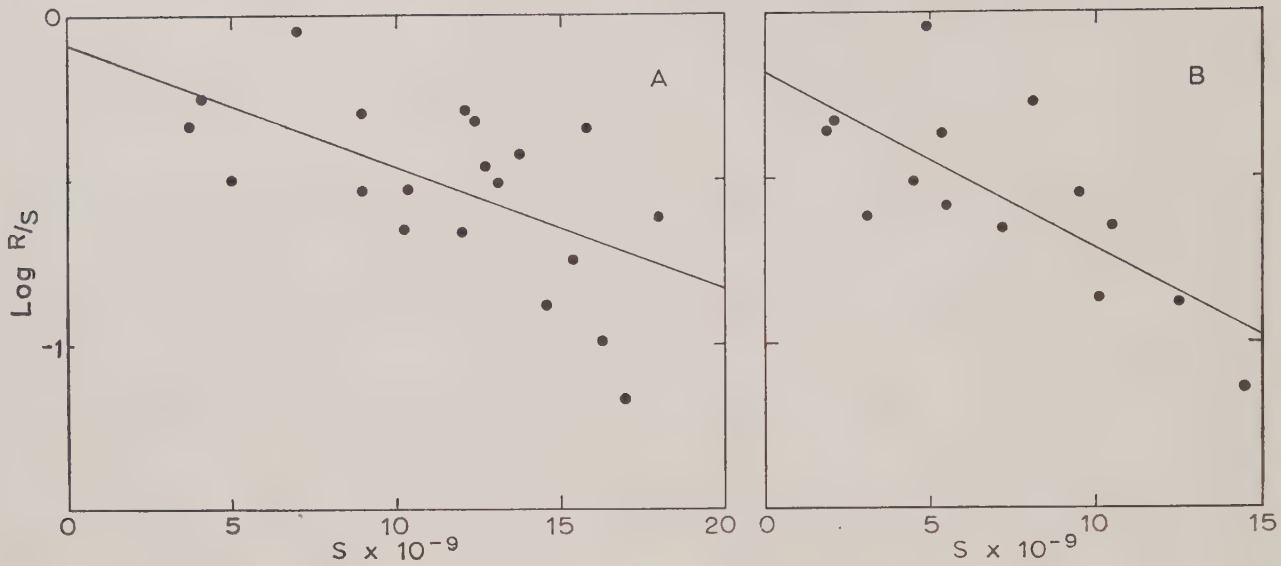

Fig. 7. *Relationship between the log ratio of recruitment to parent stock on parent stock, derived from the data of Figure 6. The negative regressions are significantly different from zero, using:* A. *Downs catches;* B. *Southern Bight catches.*

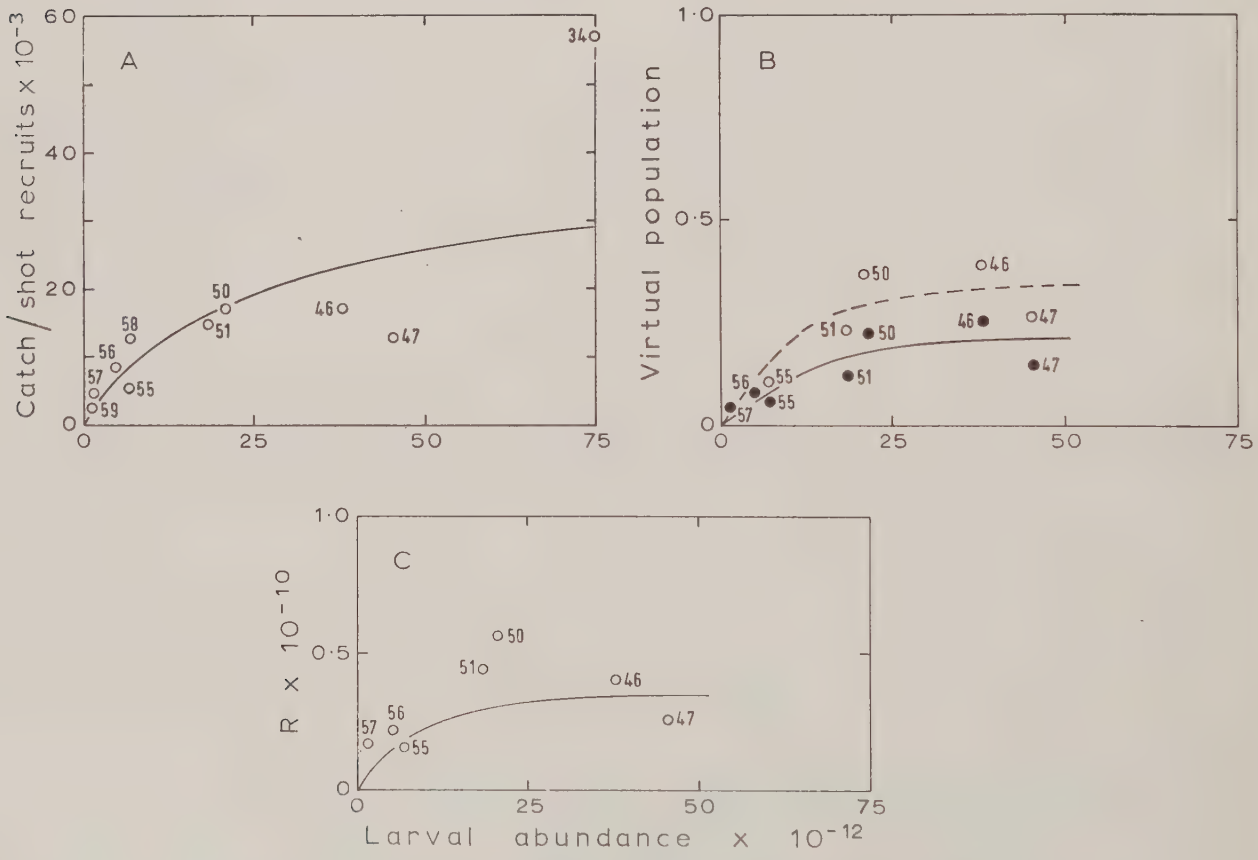

Fig. 8. *Dependence of recruitment upon larval abundance, or stock.*
A. *Recruitment as stock density in numbers corrected for the efficiency change;*
B. *Recruitment as virtual population, using estimates derived from Downs catches (– – –) and from Southern Bight catches (——);*
C. *Recruitment as stock; the curve is fitted by the method of Beverton and Holt* (1957). (*Downs catches.*)

Bight catches (excluding the proportions caught in the northern and central North Sea). Figure 8C shows the dependence of recruitment, as a stock estimate, upon the larval abundance. It will be noticed that the values for the 1934 and 1935 year-classes are absent from Figures 8B and 8C. This is because the Downs catches are available only back to 1937, and recruitment was not complete until 1938 for the 1934 year-class.

Each of the three estimates of recruitment shows the same form of dependence upon larval abundance, a convex curve rising to an asymptote fitted by eye in Figures 8A and 8B. In Figure 8B, the curve is of the same form whether the Downs catches or the Southern Bight catches are used to estimate the virtual populations. The curve fitted to Figure 8C is that using Beverton and Holt's (1957) formulation, taking reciprocals of recruitment and stock; there is a significant correlation between the reciprocal of stock and that of recruitment. The three curves, of the same asymptotic form, using different data treatments, provide evidence of a density-dependent mortality occurring amongst large recruit year-classes. The density-dependent mortality occurs *after* the age of the stage II larvae (8–12 mm), because there is no such curve in the relation between parent stock and the abundance of stage II larvae.

The figures given in Figure 8 are probably the best representation of the stock and recruitment relation in the Downs herring. They show quite clearly that the reduced recruitment did not start until the 1952 year-class, and that the subsequent ones are all low, whichever method of estimating the recruitment is used. This expresses the same point as Figure 3 (but does not add to it), showing the date by which the decline in recruitment may have started.

In the range of data in recent years (from 1955 onward), before the curve reaches the asymptote, it should be possible to predict recruitment from estimates of larval abundance. If this is true, it is likely that most, if not all, of the fish derived from Downs larvae return to spawn on their native ground. A further conclusion is that the simplest explanation of the reduced recruitment is that the stock has been reduced by heavy fishing (Cushing, Part II; Herring Assessment Group Report, 1964).

THE BRIDGER HYPOTHESIS IN THE STOCK/RECRUITMENT RELATION IN THE DOWNS HERRING

Bridger (1961) tried to account for the fact that since 1946 larval abundance had declined three to four times more rapidly than had stock density. Stock density was expressed as numbers/shot raised by an earlier efficiency factor described in Cushing (1959). In a paper to ICES in 1960 Bridger pursued the argument; Figure 9 shows the data as then presented. In Figure 9A larval abundance is plotted on spawning power (stock density $\times$ fecundity) of fish of five years of age and older. In Figure 9B larval abundance is plotted on the spawning power of the total stock, i.e. three-year-old fish and older. The intercept on the abscissa, which appears when the stock densities of three- and four-year-old fish are added to those of the older fish, suggests that the younger fish do not produce viable larvae. The two regressions are significantly different, but the intercepts on the abscissae are not so. Yet the difference in the slopes of the regressions suggested that the younger fish do not produce viable larvae.

Figures 10A and 10B show the data of Figure 9, together with some later results, corrected by the use of the efficiency factor derived from Figure 1. Larval abundance is plotted on number of eggs/shot raised by the efficiency factor. In Figures 10A and 10B the two regressions are significantly different, but the intercept in Figure 10B is not significantly different from zero. Figures 10C and 10D show larval abundances plotted on Downs stock of ages 5–9 and ages 3–9, respectively. Again, the regressions are significantly different, but in this case the intercept in Figure 10D is significantly

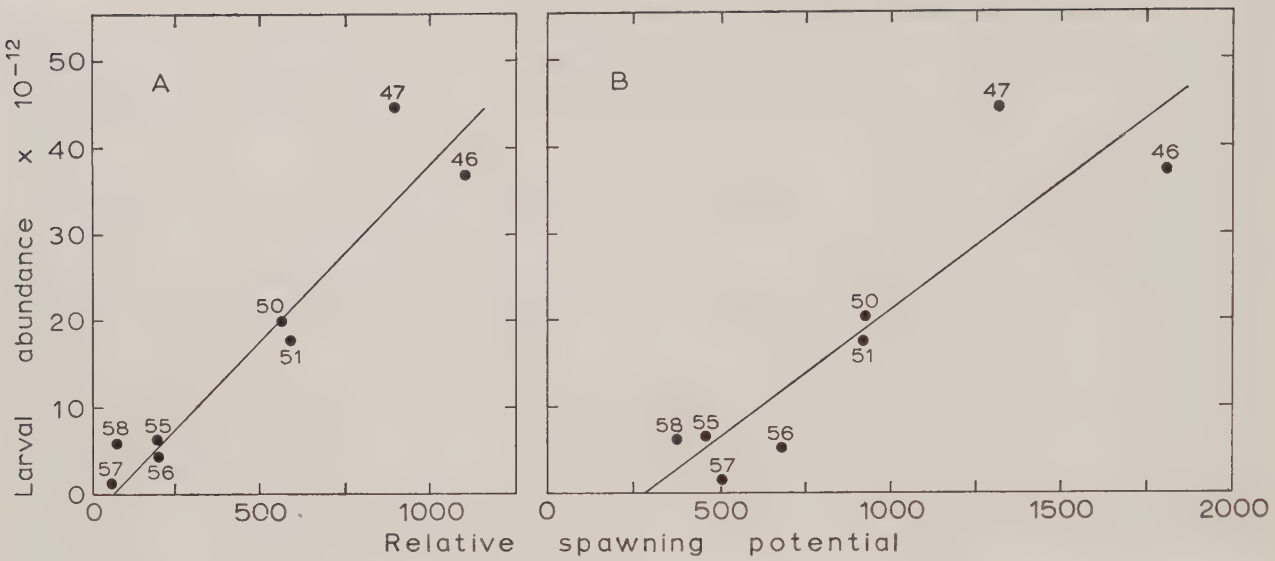

Fig. 9. A. *Dependence of larval abundance upon spawning power (from Bridger, 1960), using:* A. *Stock densities of fish of five years of age and older;* B. *Total stock densities (of fish of all ages, three to nine).*

different from zero. It is concluded that the larvae of younger parents are less viable than those of older ones. This conclusion is not generated by the use of numbers/shot as stock indices.

It will be recalled that spawning power is defined as stock density (in weight) × fecundity, or alternatively as number of eggs/shot. So Figure 10A can be regarded as a correlation between stock density and abundance. It is a correlation significantly different from zero (p 0·01), showing that stock density is a good relative index of abundance. Because larvae die, the slope cannot be used to estimate q, the catchability coefficient. However, the very important conclusion remains that stock densities of herring, a pelagic and shoaling species, can be used with confidence to estimate relative changes in abundance.

The second important conclusion from this piece of work is that the younger herring may produce larvae that are not viable. The decline in larval abundance since 1946 was three to four times greater than the decline in crude stock density as the East Anglian driftermen became more efficient. Given the efficiency change, the difference between larval abundance and stock density disappears and a decline in recruitment is revealed.

There is a third conclusion, already referred to above, that any compensatory mechanism in the stock and recruitment relationship must be found between the age of larval capture and recruitment, and not between the age of hatching and that of larval capture.

There are biological difficulties in accepting the apparently poor viability of eggs or larvae from three-year-old fish; the work of Blaxter and Hempel (1963) on this very problem illuminates them. The main effect of the recruitment change in 1950–2 was to make the dominant year-class the three-year-old herring rather than the four- or five-year-old fish of earlier years. If the three-year-old fish did produce non-viable larvae, the effect should have been first noticeable in 1955. Very low numbers of larvae were in fact first recorded in the period from 1955 onwards and it was at this time that recruitment became significantly reduced. It is this sequence of events, supported in Figure 3 and in Figure 9, which relates the stock/recruitment relation to the phenomenon expressed in Figure 10D. The Bridger hypothesis, when formulated, tried to account for differences between stock density and larval abundance. The efficiency change resolves this difference and the Bridger hypothesis is now extended to try to explain the stock/recruitment relations.

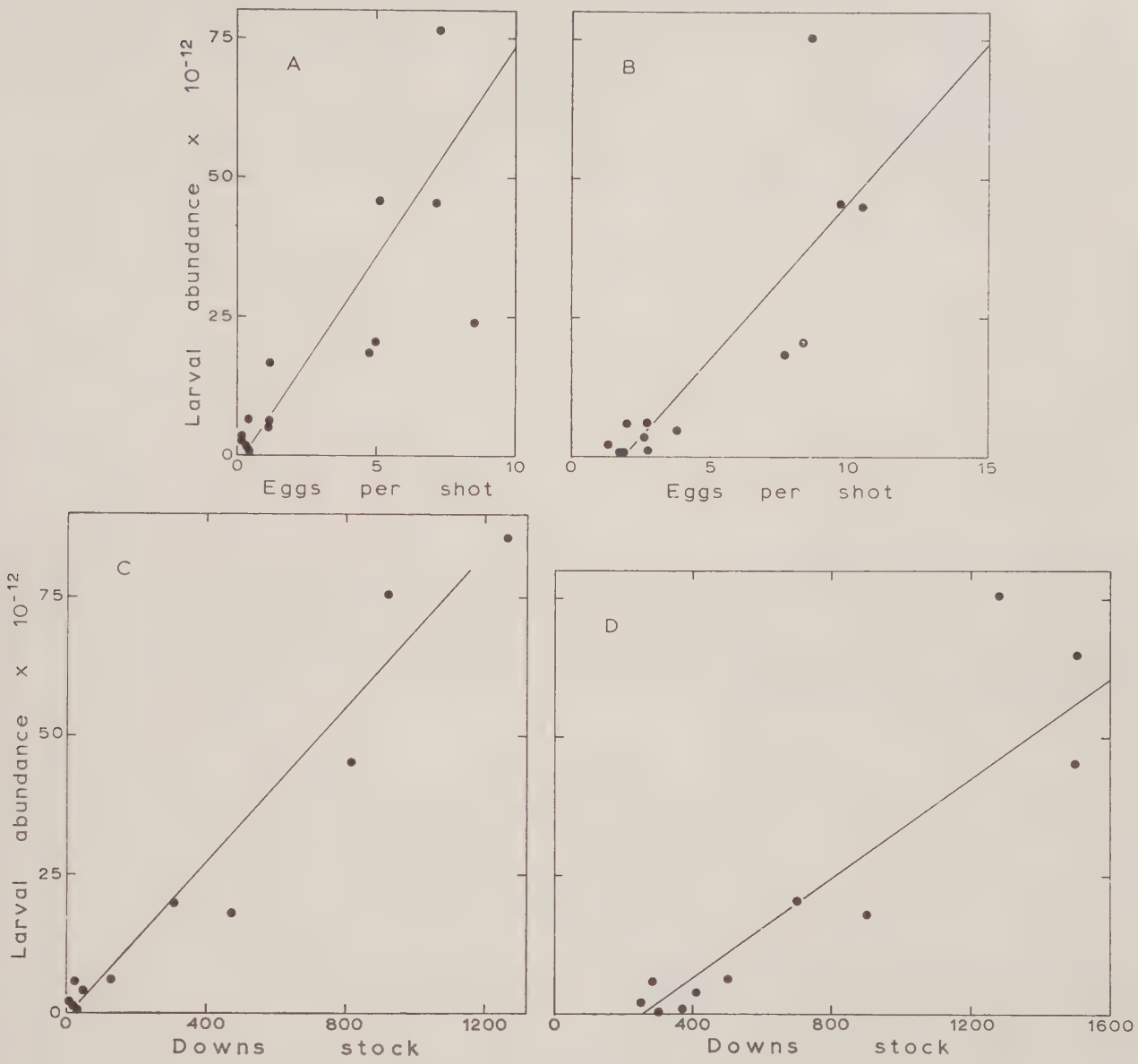

Fig. 10. *Dependence of larval abundance on stock and stock density.*
A. *Stock densities of fish of five years of age and older, corrected by the efficiency factor.*
B. *Total stock densities (ages three to nine), corrected by the efficiency factor.*
C. *Downs stock in numbers, ages five to nine.*
D. *Downs stock in numbers, ages three to nine.*

Blaxter and Hempel (1963) have noted a correlation between the length of the mother fish and the dry weight of the egg laid; the egg laid by a three-year-old fish is 10% less in weight than that of a five-year-old fish. It has also been shown by these authors that larval survival under experimental conditions depends on egg weight. So, if there were competition for food between large and small larvae, the smaller offspring of the three-year-old parents would be at a disadvantage. The difference in survival noticed by Blaxter and Hempel is very small, being one or two days in 50% survival in a period of about 24 days under conditions of starvation. It remains questionable whether an innate difference of such small magnitude could generate mortality of competitive origin in the first month or so of larval life.

Rigorous demonstration that the larvae produced by three-year-old fish are vulnerable might be difficult. However, the mortality from eggs to larvae can be estimated and then correlated with the percentage of three-year-olds in the catches.

At the beginning of the year, let stock in numbers be N.

At the end of the year, let stock in numbers be Ne^{-Z}.

During the year, let the catch in numbers be C.

By the end of the year,

$$C = \frac{F}{Z}(1 - e^{-Z})\, N,$$

so

$$N = C \cdot \frac{Z}{F} \cdot \frac{1}{(1 - e^{-Z})}$$

and

$$Ne^{-Z} = \frac{C \,.\, Z \,.\, e^{-Z}}{F(1 - e^{-Z})} \,.$$

For all years when larval surveys were made, the weight for age and fecundity for age are known. So the catches (as Downs catches or as Southern Bight catches), can be split by ages, using the percentage age-compositions. Half the catch of each age (in g) is divided by the weight for age (in g) to give the numbers of females and then multiplied by the fecundity to give the number of eggs in the catch. This quantity is then raised by

$$\frac{Z}{F} \cdot \frac{e^{-Z}}{(1 - e^{-Z})}$$

to give the number of eggs in the stock of that age. The stock of eggs for all ages is summed:

$$\sum_{n=3}^{n=9} \frac{C_i \,.\, 10^6}{2w_i} \cdot f_i \frac{Z}{F} \cdot \frac{e^{-Z}}{1 - e^{-Z}} \,,$$

where C_i is the catch of age-group i in tons,

where w_i is the mean weight of fish of age i,

where f_i is the mean fecundity of females of age i.

The larval surveys give estimates of the larval stock, and so the mortality from the time of laying to the time of capture of larvae can be estimated. It will be recalled that the early surveys tended to be less well sampled in space and time than those from 1956 onward, so underestimating the larval abundances in earlier years. If this is so, then the estimates of mortality in the earlier years will be biased upwards. Figure 11 shows the relation between 'egg to larva' mortality and the percentage of three-year-old fish in the catches ($r = 0{\cdot}70$; p 0·02 for Downs catches; for Southern Bight catches, $r = 0{\cdot}93$; p 0·01). When the proportion of three-year-old fish is high, so is the larval mortality. Because the high proportion of three-year-olds is found in the second half of the time series (when mortality was well estimated), the overestimate of mortality in the first half due to poor sampling may be disregarded. Hence it appears that the larvae of three-year-old fish suffer heavier mortality than those of older fish. But it should be noted that this correlation is based on parallel time series. However, the evidence in Figures 10 and 11 combined makes it hard to avoid the conclusion that the larvae of younger parents suffer heavier mortality.

The evidence given in Figure 11 leads us to believe that the larvae of three-year-old fish are considerably less viable than those of five-year-old parents, even if the precise causes remain unknown. Consequently if there were any form of correlation between larval abundance and subsequent recruitment, the decline in recruitment is shown to have a biological origin, although the reduction in stock could well be due to fishing. When the stock is reduced almost to a single year-class of three-year-olds by fishing, then the stock becomes exceedingly vulnerable to recruitment failure.

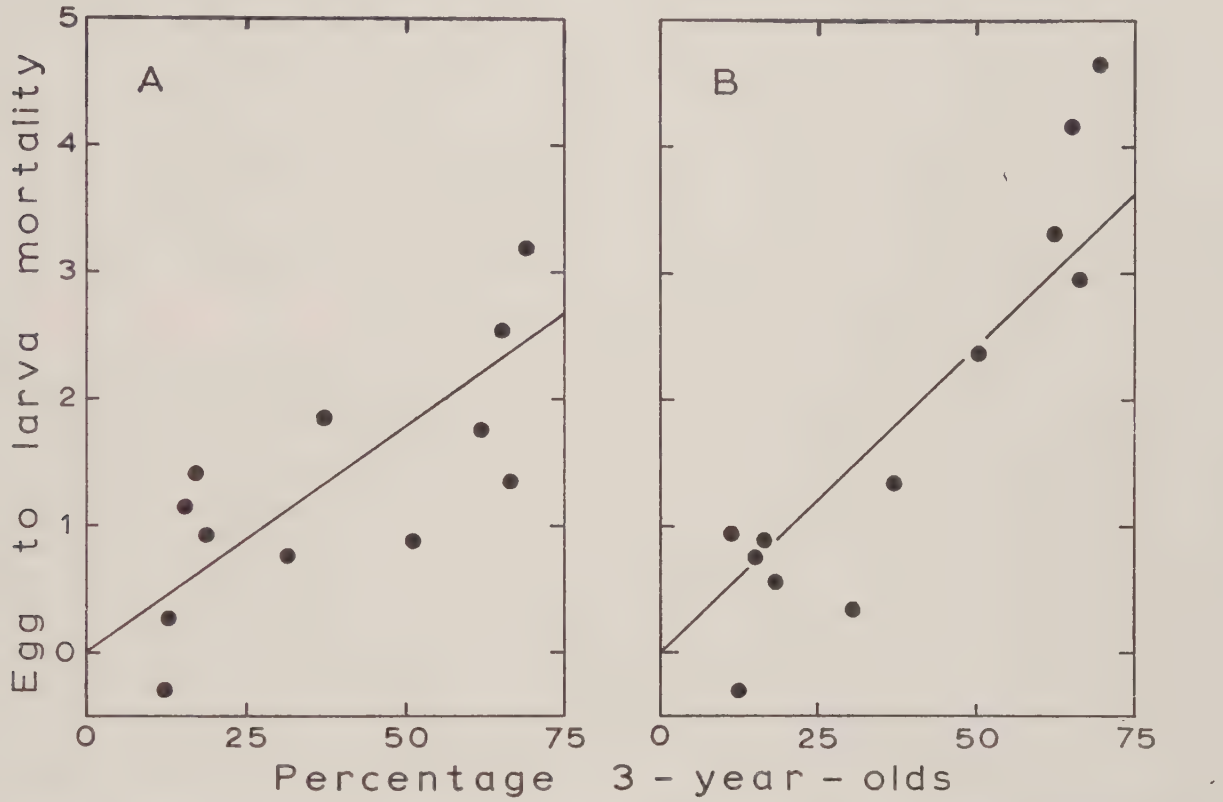

Fig. 11. *Relation between 'egg to larva' mortality and the percentage of three-year-old fish in the catches, using:* A. *Downs catches to make the estimate of numbers of eggs;* B. *Southern Bight catches to make the estimate of numbers of eggs.*

THE POSSIBLE CAUSES OF THE DECLINE IN RECRUITMENT TO THE DOWNS STOCK

If there is a relationship between stock and recruitment, recruitment can be reduced by natural causes or by fishing. In any such case, it is hard to distinguish a natural cause from the effect of fishing. In this case there are three added complications: firstly, the effect of the Bløden fishery on recruitment, secondly, the observed natural changes in recruitment in the North Sea herring since the war (in pattern for the Downs stock and in quantity for the Buchan stock), and thirdly, the marked effect of fishing on the Downs stock (Cushing, in Part II).

THE POSSIBLE EFFECT OF THE BLØDEN FISHERY

The possible rate of reduction of recruitment on the Bløden ground is also probably the proportionate rate to all the North Sea autumn-spawning stocks (Cushing, 1959). The fishing mortality during the Bløden fishery was shown by an international tagging experiment to have been 16·5% in 1957 and 18·5% in 1958 (Aasen *et al.*, 1961). It is possible that these percentages are overestimates, because there are regions where immature herring live in the North Sea which are not fished during the Bløden fishery; yet the fish in some of these areas must pass through the Bløden fishery. It is also possible that tagging mortality, for which a correction was made, was underestimated. Because a choice cannot be made of these possibilities, the rough value of 15–20% will be used here.

In Cushing (1959) another method was used in estimating the effect of the Bløden fishery on the Downs recruitment. Given the proportion of the Downs stock in the North Sea autumn-spawning stocks, and hence in the Bløden fishery, and the mortality between the Bløden fishery and the East Anglian fishery, the loss to the Downs stock can be obtained by expressing the Downs part of the Bløden catch as a proportion of the Downs stock. In Cushing (1959) a range of proportions of Downs stock to North Sea stock was calculated, varying from 0·1 to 1·0; the effect of a range of natural mortalities from 0·25–1·0 was treated separately.

Popp Madsen (personal communication) has estimated that the natural mortality of the herring between the Bløden fishery and the adult fishery is 0·45. This estimate was made by taking the ratio of the Bløden stock to adult stock, both in numbers. It will tend to be an overestimate because there are immature stocks unexploited by the Bløden fishery, but perhaps it is not too much of an overestimate, for the reasons given above. In the North Sea Herring Working Group Report (ICES, 1965) estimates are given of the proportions of the three spawning groups in the North Sea (Buchan, October Dogger, and Downs); it is suggested that in the period of the late fifties the three stocks were of the same size. The data used were those given in Figure 12, uncorrected for efficiency changes. Figure 12 shows the recruitment to each of the three North Sea stocks for fairly long time periods. It will be recalled that the Buchan spawners and Downs spawners were sampled by driftermen and that the October Dogger spawners were sampled by trawlermen; the latter samples were corrected for power changes. The efficiency change described above was probably associated with the use of echo-sounders, radio and Decca – which are not incorporated in the power correction. Hence there is a case for considering the data in Figure 12 as comparable between stocks. The proportion of one third for the Downs stock given in the North Sea Herring Working Group Report will be considered a maximum for the period of the late fifties. In view of the decline in recruitment effective after 1954, it is possible that the true proportion for the second half of the fifties lies between one third and one sixth.

Figure 13 shows the percentage loss to the Downs stock due to the Bløden fishery, with the assumptions given above. Then the loss is estimated by taking one third of the Bløden catch (reduced by a natural mortality of 0·45, for the period between the Bløden fishery and the East Anglian fishery) as a proportion of the Downs (or Southern Bight) stock. It has been calculated in two ways: (*a*) using the Downs catch to estimate the stock of three-year-old fish, (*b*) using the Southern Bight catch to estimate the stock of three-year-old fish. Thus the proportion of the Downs stock mixing in the northern and central North Sea can be allowed for, taking the Downs catch as the maximum and the Southern Bight catch as the minimum. It will be seen that the Southern Bight catch estimates yield a higher loss rate than the Downs catch estimates, as might be expected. Then if the proportion of one third as stock proportion is too high, the percentages should be reduced accordingly.

Figure 13 also shows the fishing rates, as estimated by the international tagging experiment (given as crosses), and these are quite close to the Downs catch estimates. Figure 14 gives a relationship between the percentage loss to the Downs stock and the catch on the Bløden ground. When the

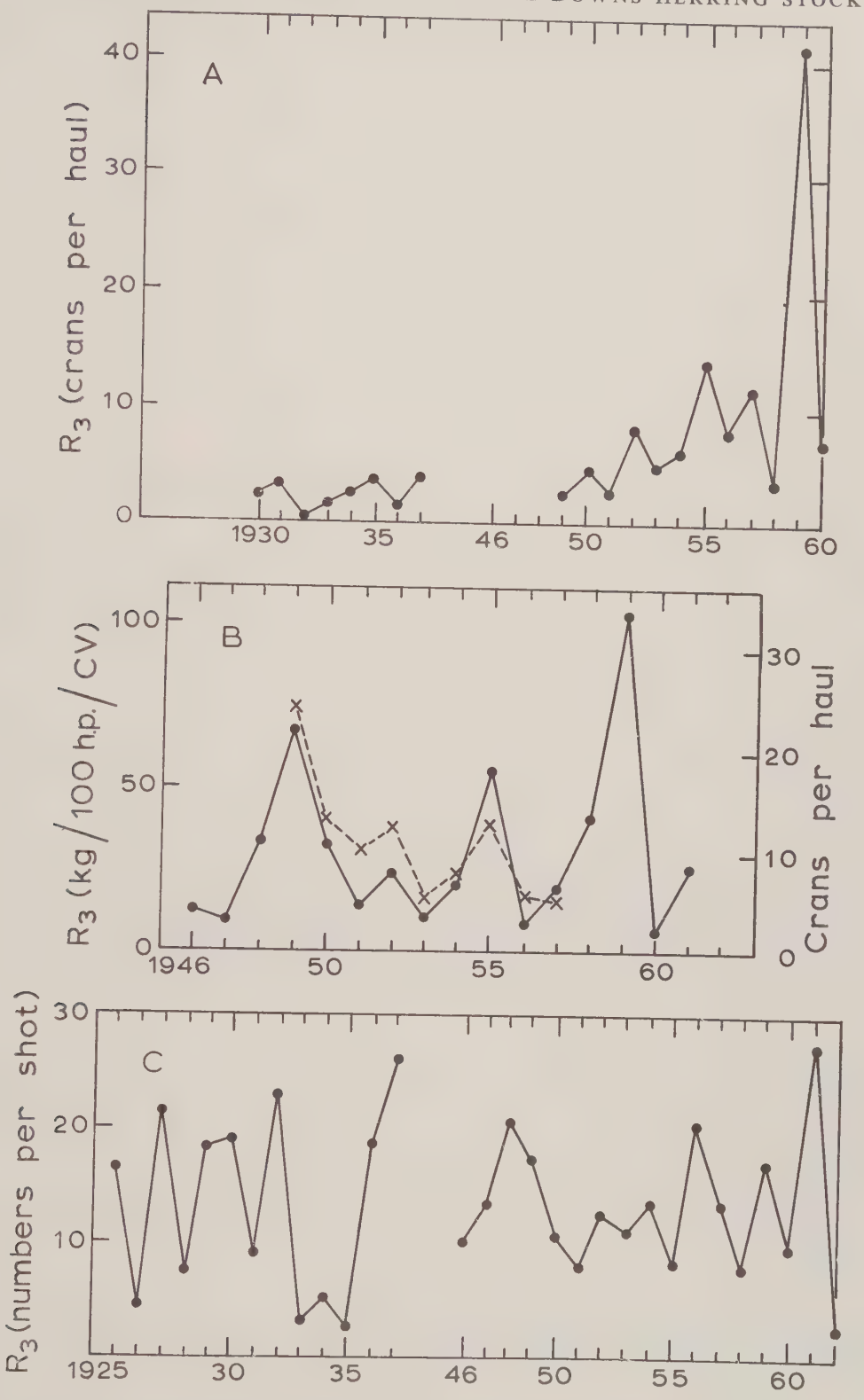

Fig. 12. *The total recruitment, as at three years of age (as estimated by Cushing in Part I), to the three main North Sea stocks: A. Buchan spawners; B. October Dogger spawners; C. Downs spawners. The estimates in C are not corrected by the efficiency factor.*

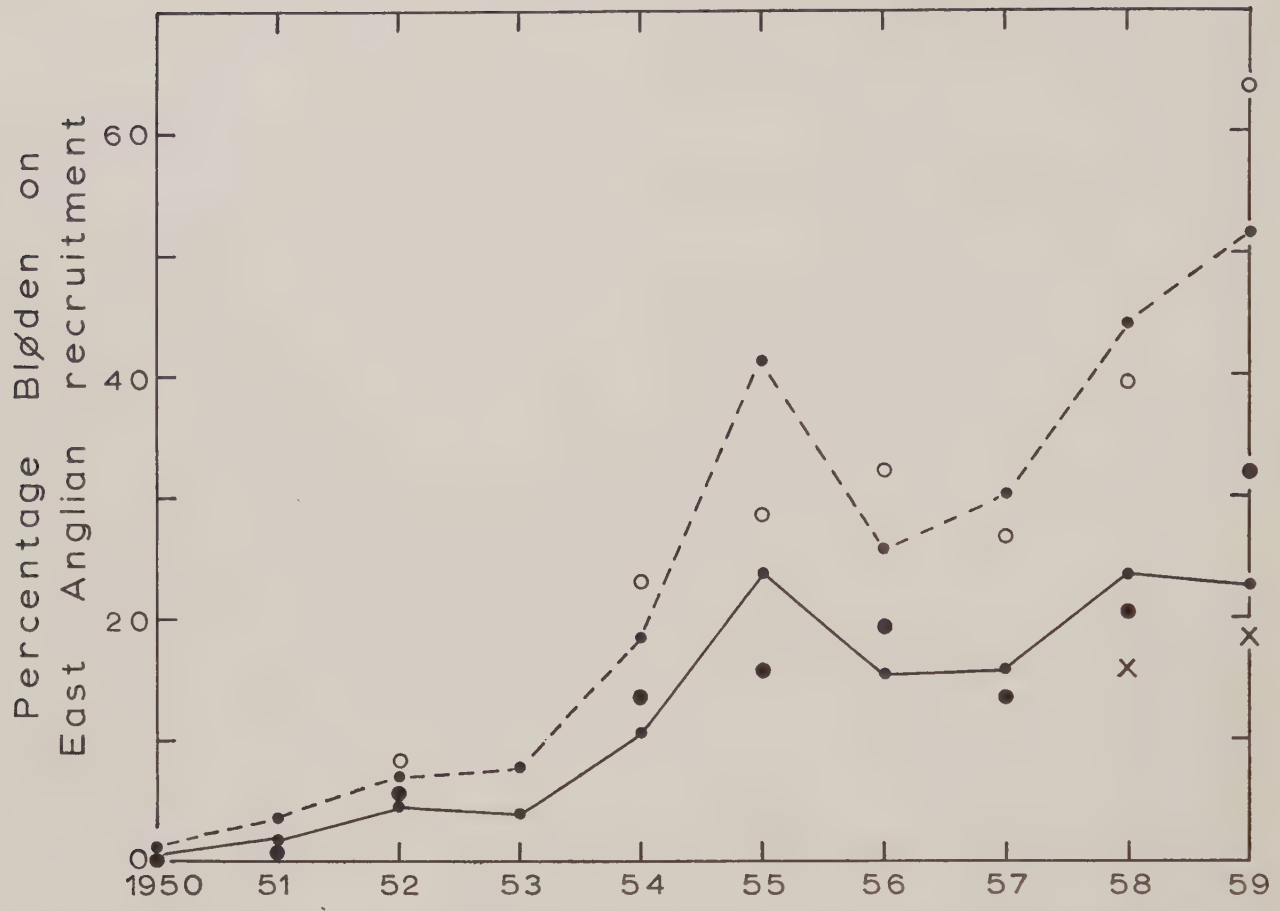

Fig. 13. *The percentage loss to the Downs stock exerted by the Bløden fishery, using Cushing's* (1959) *method with the modifications described in the text. The full line gives the estimate derived from Downs catches and the broken line gives that derived from Southern Bight catches. Mortality rates from the East Anglian fishery were averaged from* 1950–5 *and from* 1955–60. *The open circles represent estimates of percentage loss to the 'Southern Bight' stock, using actual mortality rates from the East Anglian fishery. The solid circles represent estimates of percentage loss to the Downs stock, using actual mortality rates from the East Anglian fishery. The crosses give the percentage fishing rates on the Bløden ground (from ICES tagging experiment, Aasen et al.,* 1961) *in* 1958 *and* 1959.

Bløden catch reaches $1{\cdot}6 \cdot 10^9$, the loss is 15%. Combining the two figures it is seen that the effective loss could be taken as starting in 1954. If the percentage fishing rate from the tagging experiment were an overestimate, then the 'Downs catch' value is too high because of three possibilities:

(*a*) the Downs proportion on the Bløden ground is underestimated;
(*b*) the natural mortality of the immature herring has been overestimated;
(*c*) the proportion of adult fish mixing in the northern and central North Sea has been underestimated.

It is likely that the Downs proportion in the Bløden catch is overestimated between 1955 and 1960, in view of the decline in stock. It is likely that the natural mortality of the herring between the immature and adult fisheries has not been overestimated. Hence, the percentages given in Figure 13 are higher than expected.

As compared with the pre-war recruitment, that in the period 1955–8 (year-classes 1952–5) was reduced by about two and a half times, or by 60% (see Figure 3, which probably gives the best estimate of the decline of recruitment). The question is whether the Bløden fishery can account for

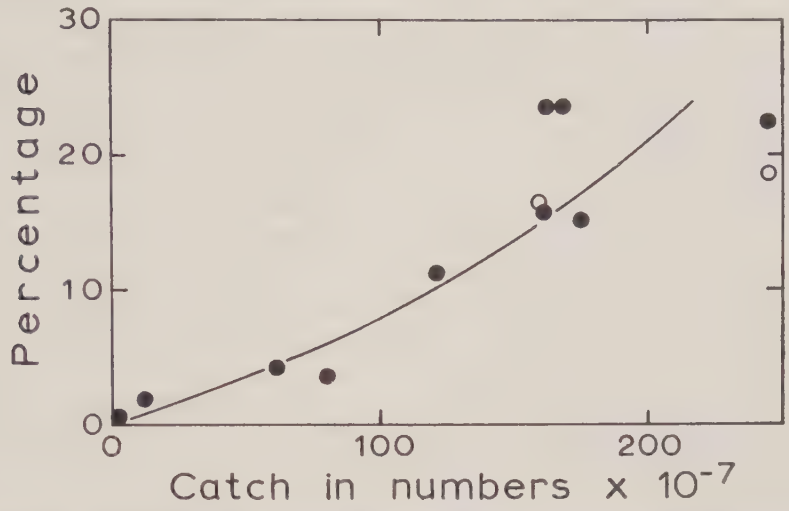

Fig. 14. *The relation between the percentage loss to the Downs stock and the Bløden catch in numbers. The open circles show the percentage fishing rates for the catches in* 1957 *and* 1958 (*from Aasen et al.*, 1961).

this decline. The figures given above, tentative though they may be, suggest that this is not so. It is thought that 20% is perhaps an upper limit, which is a third of the value required. The first significantly low year-class is that of 1952, reaching the Bløden fishery in 1954 and the East Anglian fishery in 1955. As this is the first year-class in the period of high Bløden catch, doubt must remain. However, from the evidence we have of the steadily falling Southern Bight catches ($<$100,000 tons in 1961, 1962 and 1963), it is likely that the recruitment has continued to decline. During this period the Bløden fishery has fallen and indeed the spring fishery has stopped (Popp Madsen, personal communication). This was to be expected if recruitment was reduced before the age of the Bløden fishery, but not if the Bløden fishery causes the reduction in recruitment directly. This is the picture given in Figure 9, relating recruitment to the earlier larval abundance.

The question whether the Bløden fishery can account for the observed decline in recruitment cannot be answered decisively. However, it can be said that the best estimate of the effect is a reduction of 20% in recruitment, as compared with the required reduction of 60%. If the proportion of adult Downs fish mixing in the northern and central North Sea is considered a maximum, if the Downs proportion on the Bløden is one third or less, and if the estimated mortality of the immature herring is 0·45 or greater, then the estimate of 20% is perhaps a little high. As noted above, the estimate of 15–20% from the international tagging experiment may be biased upward or downward. In the face of this kind of evidence it is thought that the Bløden fishery does not account for the observed decline in recruitment.

THE POSSIBLE EFFECT OF THE OBSERVED NATURAL CHANGES IN RECRUITMENT

In Figure 12 are shown the changes in recruitment, uncorrected for the efficiency change; in Figure 2 is given the decline in recruitment to the East Anglian fishery. From 1925 to 1961, in Figure 12, the uncorrected observations for the Downs stock show no upward or downward trend. Again from 1944 to 1958 the same type of observations for the October Dogger stock show no upward or downward trend. But for the Buchan spawning stock, there was an increase in recruitment in 1952; in the subsequent years, the increase amounted to about three times.

As the year-classes of 1947, 1948 and 1949 recruited to the Downs stock, so did the pattern of recruitment change, the age at first recruitment being reduced from 3·5 to 3·0. This change was associated with an increase in growth, effective in 1950–2 and subsequently. The same sort of changes occurred in the other two spawning stocks, as a reduction in the age of first recruitment associated with an increase in growth. Perhaps the increase in the quantity of recruitment to the Buchan stock was associated with the same cause. The catches on the Bløden ground increased from merely small quantities (about 5 000 tons) to large weights (30 000 tons +), at about the same time. The growth change was sharpest at this time and was associated with an increase of *Calanus* in the southern North Sea, and, as Colebrook (1963) has shown, on the Bløden ground. It is clear from Figure 3 that the decline in recruitment to the Downs stock was first noticeable by 1955 – the 1952 year-class. For a simple diversion of recruits from one stock to another, at the same time as the increase of the Buchan stock, this is three years too late. Nor is there a simple inverse correlation between the recruitments to the Downs and Buchan stocks since the 1949 year-class. Indeed there is no correlation of any sort between the whole range of data, in crude stock density or in stock density corrected for efficiency changes. The possibility remains that a complex and undetected wastage of Downs recruits has taken place to the other two spawning groups. This might be held to account for the high vertebral counts found in the Buchan spawning group in recent years, but it would not account for the low (and in one year-class, 1956, excessively low) K_2s (keel scale counts) found there. Further, there is no sign of augmentation to the Dogger stock in the crude stock density figures (Figure 3) as might be expected if there had been a wastage of the Downs recruits to the north.

Figure 8 shows the relationship between larval abundance and the recruitment three years later. It has been suggested in the previous section that this relationship can only emerge if the majority of spawners return to their native grounds to spawn. One might suggest that the recruits had emigrated, but one would then have to explain the reduced larval abundance. Indeed the stock and recruitment relation could be explained as a 'decline in recruitment', recruitment coming from elsewhere. But Figure 8 shows a decline in recruitment dependent on reduced larval abundance – which must mean that the recruits originated from those larvae. Similarly Figure 11 shows that the larvae are related to parent stock. Hence the stock and recruitment relation is most probably one within the Downs stock, with no external source of recruitment.

If the majority of herring return to their native grounds to spawn, the Downs stock and the other two, Buchan and Dogger, are distinct in every sense. Zijlstra (1958) first suggested that this was so. Cushing and Burd (1957), Burd and Cushing (1962) and Cushing (in Part I) have shown that the Downs stock is a unit as a year-class of adults, returning to the ground of first spawning, until the year-class is extinguished. Hence the possibility that the herring do return to their native grounds to spawn has not been unforeseen.

Although, in a speculative sense, the wastage of recruitment to the other two stocks could have taken place, it is a little difficult to show that it has done so. Evidence of meristic characters militates against the possibility of the movement of Downs recruits into the Buchan spawning fishery. Hence it seems unlikely that the natural changes in growth and recruitment observed in the early fifties had any great effect on the decline of recruitment to the Downs stock. It is, of course, always possible to postulate the unnamed natural cause, but the resolute search for it reveals only the contrary evidence.

THE DECLINE IN RECRUITMENT AS A CONSEQUENCE OF THE DECLINE IN STOCK DUE TO FISHING

Cushing (in Part II) has shown that, in the Downs stock, $F/Z \simeq 0{\cdot}75$. Zijlstra and Postuma (1963) have shown that throughout the whole North Sea the effect of fishing is probably the dominant

cause of mortality. In the Downs stock, $Z \simeq 1{\cdot}00$ during the second half of the fifties (Herring Assessment Group Report, 1964). There is considerable evidence that $M \simeq 0{\cdot}25$ (summarized by Cushing, in Part II); indeed, Postuma (1963) suggests that M could be as low as 0·08. In the first half of the fifties, $Z \simeq 0{\cdot}75$. So during the whole decade, $F/Z \simeq 0{\cdot}66$–$0{\cdot}75$. In the twenties and thirties, it is likely that $F/Z \simeq 0{\cdot}5$; $F \simeq 0{\cdot}25$; $M \simeq 0{\cdot}25$. Comparing the pre-war period with the fifties, total mortality had doubled, and by the late fifties fishing mortality had trebled.

Given the stock and recruitment relation shown in the previous section, a reduction in stock must generate a reduction in recruitment. Hence the reduction in stock of two to three times since the thirties is sufficient to account for a reduction in recruitment of about the same order. The reduction in stock is due to fishing and so the simplest explanation of events is that the reduction in recruitment is due to the same cause.

It has been shown that the mortality of larvae has increased sharply, probably with the increased proportion of three-year-old fish in the fishery. It has been shown that the reduction in stock, leading to a stock of three-year-old fish only, is due to fishing. Hence, as fishing reduces the stock, the larval mortality must be expected to increase. It has been shown that the dependence of recruitment on larval abundance, or stock, has fallen from the asymptote since the 1952 year-class, recruiting in 1955. It is no accident that this date coincides with the recruitment change bringing predominantly three-year-old fish into the fishery. This natural change of minor importance has set in motion a decline in recruitment to the Downs stock which can be directly attributed to fishing. A reduction in the fishing effort exerted on the Downs stock would result in the reappearance of the five-year-old fish, and recruitment would be restored to its former level.

Any stock and recruitment relationship can be interpreted in one of two ways, that recruitment failure is due to reduced stock or that stock failure is due to reduced recruitment. It has been suggested above that the first alternative is the simpler. Figure 15 shows the time series of the percentage R/S, between 1947 and 1960, for the Downs stock. It is seen that recruitment, as proportion of stock, increased steadily during the period. Therefore stock failure occurred first and recruitment failure followed as the consequence. If recruitment had failed first, a downward trend in R/S would be expected with time.

Thus it is concluded that the recruitment failure is due to reduction in stock, which is in itself due to fishing.

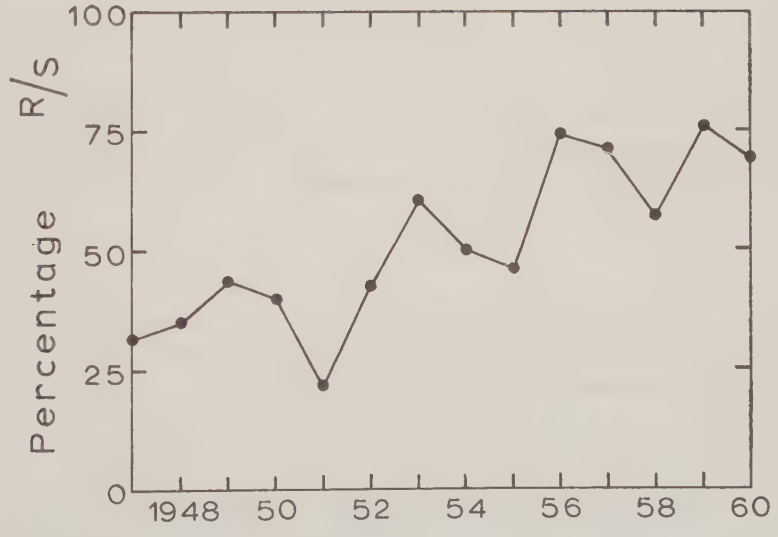

Fig. 15. *Time series from* 1947–60 *of the percentage* R/S *for the Downs stock.*

DISCUSSION

THERE are two important questions that arise from this paper:

1. What is the relation between the decline in recruitment and the increase in efficiency?
2. Do the events described occur in other herring populations?

Because the decline in recruitment was of the same order as the increase in efficiency, it remained undetected. They are independent events, as shown in Figures 1 and 3, although for some purposes they can be treated as having the same sort of effect. From the evidence given on the correlation between egg-to-larva mortality and the percentage of three-year-olds in the catches, and from Figure 3, it seems that the recruitment decline dates from the 1952 year-class, reaching the East Anglian fishery in 1955. One would imagine that if the efficiency change had been associated with the use of echo-sounders, radio and Decca, it would have started before 1955, as indeed is shown in Figure 1.

Thus the decline in recruitment and the increase in efficiency were independent events. It remains possible however that, as abundance declined, driftermen extended their searching operations with the post-war electronic aids. The fact that the decline in recruitment was of the same order, inversely, as the increase in efficiency, must be considered a coincidence.

Data on larval abundances in other herring populations have not yet been collected sufficiently widely or frequently to provide the sort of evidence given in Figure 8. Figure 16A gives the relationship between stock and recruitment in stock density for the Dogger spawners for the period 1943 to 1961 (by courtesy of Mr J. J. Zijlstra). Figure 16B shows the same data plotted as log R/S on S. Neither of the regressions in Figure 16 is significantly different from zero. It might be expected that lack of correlation in Figure 16A would be associated with correlation in Figure 16B. However, the range in stock abundance is narrow. Figure 17A shows the stock and recruitment relationship in stock density for the Buchan spawners, before and after the increase in recruitment, each period being shown separately. Figure 17B shows the same data plotted as log R/S on S. The conclusion from these data, as given, is that the other two North Sea stocks are not yet dominated by a decline in recruitment such as has taken place in the south.

However, such a conclusion might be quite misleading, if an efficiency change of the same character as that in the south should be applied to the stock densities used. An attempt has been made to make a rough estimate using measures of stock. Lengths for age from 1952 onwards are given in the North Sea Herring Working Group Report (ICES, 1965). Where lengths for age for early years were needed, the pre-1952 figures were reduced by 1 cm. The proportions of catch attributable to the Buchan and Dogger stocks, in fisheries other than the spawning fisheries, were taken from Part I. The lengths for age were converted to weights for age using $w = 0{\cdot}0085\, l^3$. The total catches in tons, by years, were separated by the percentage age distributions. The catch at each age in tons was divided by the weight at age to give numbers. These figures were summed to give numbers caught, and then raised by

$$\frac{Z}{F} \cdot \frac{1}{(1 - e^{-Z})}$$

to give stock in numbers. In both the Dogger and Buchan stocks no decline in recruitment (as stock of four-year-olds or as stock of three-year-olds) was noticed. Nor was any decline in virtual population found. Hence, tentatively, it is suggested that the Dogger and Buchan spawning groups have not yet suffered a decline in recruitment such as has been described for the Downs stock.

Ayushin (1963) has published data on the year-classes of the Sakhalin herring. Figure 18A shows the dependence of recruitment on parent stock for two periods, 1905–29 and 1930–54. Figure 18B gives the same data, as log R/S on S. There is a very marked negative regression in the latter figure, showing that the survival rate decreases markedly with increased stock. In other words, in the greatest

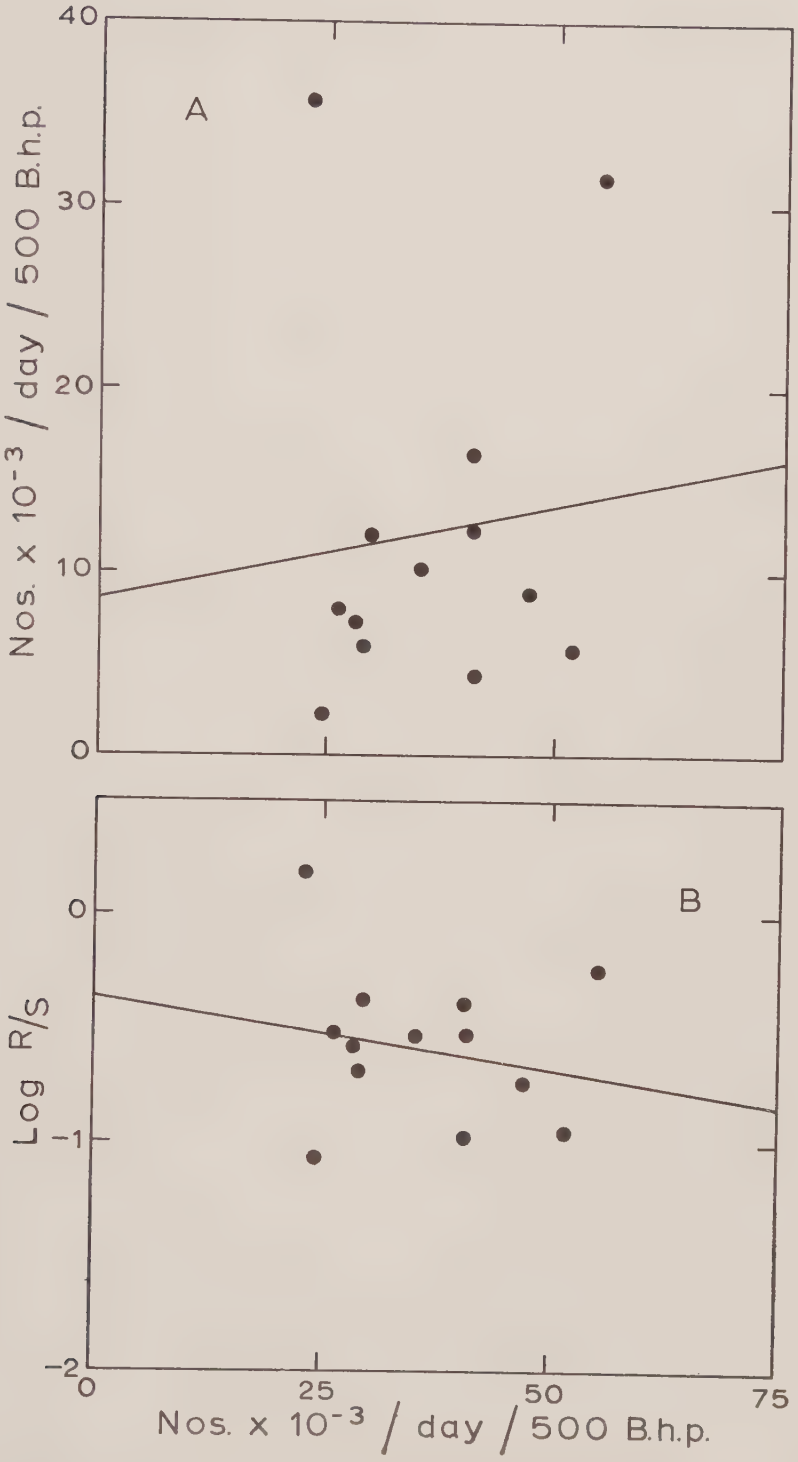

Fig. 16. A. *The relation between recruitment and parent stock for the Dogger spawners (in stock density). There is no correlation.* B. *The relation between the log ratio of recruitment to parent stock (R/S) and stock (S). The negative regression is not significantly different from zero.*

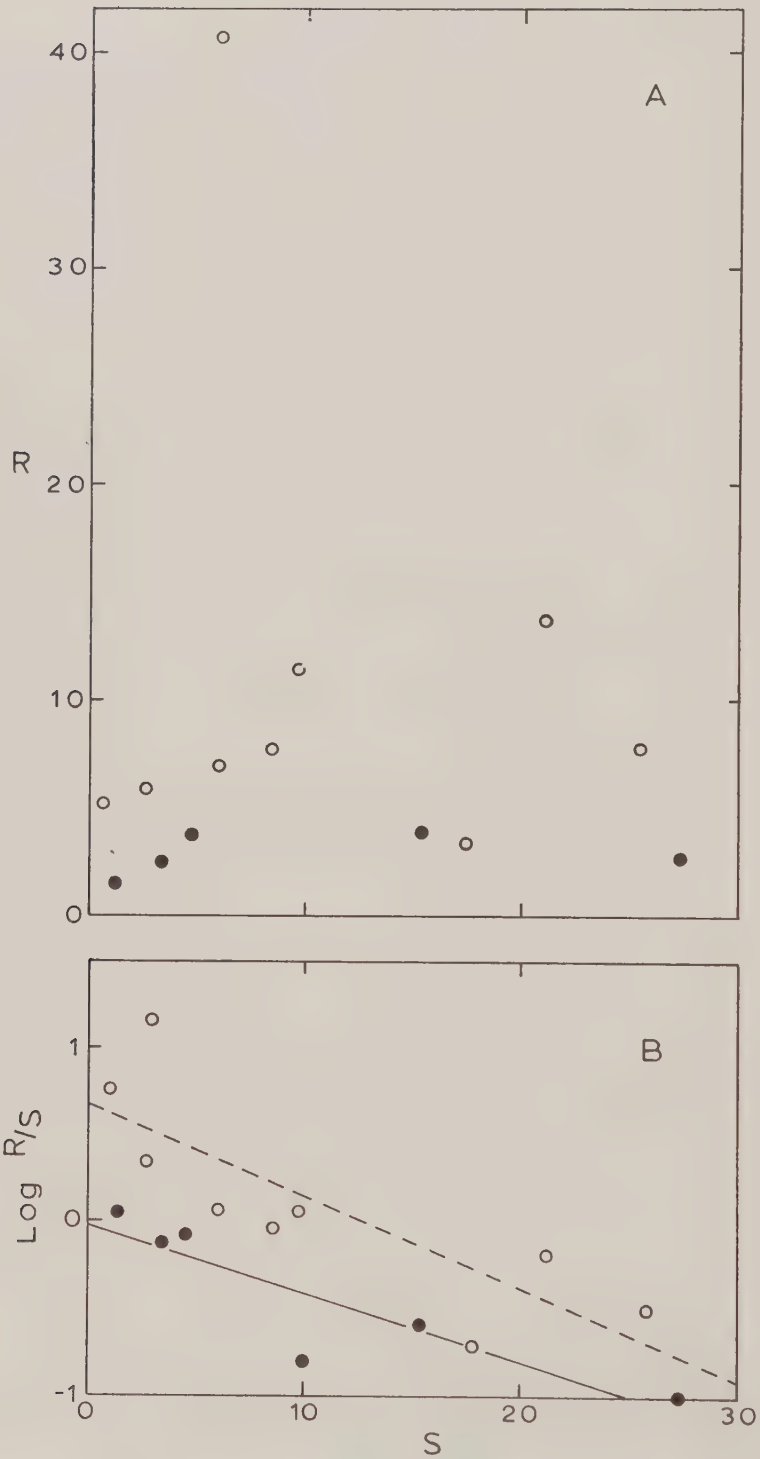

Fig. 17. A. *The relation between recruitment and parent stock for the Buchan spawners (in stock density). The data are separated into two periods,* 1930–51 *(solid circles) and* 1952–60 *(open circles). There is no correlation in either period, or in both.*
B. *The relation between the log ratio recruitment to parent stock (R/S) and stock (S). The negative regression for each of the two periods is significantly different from zero.*

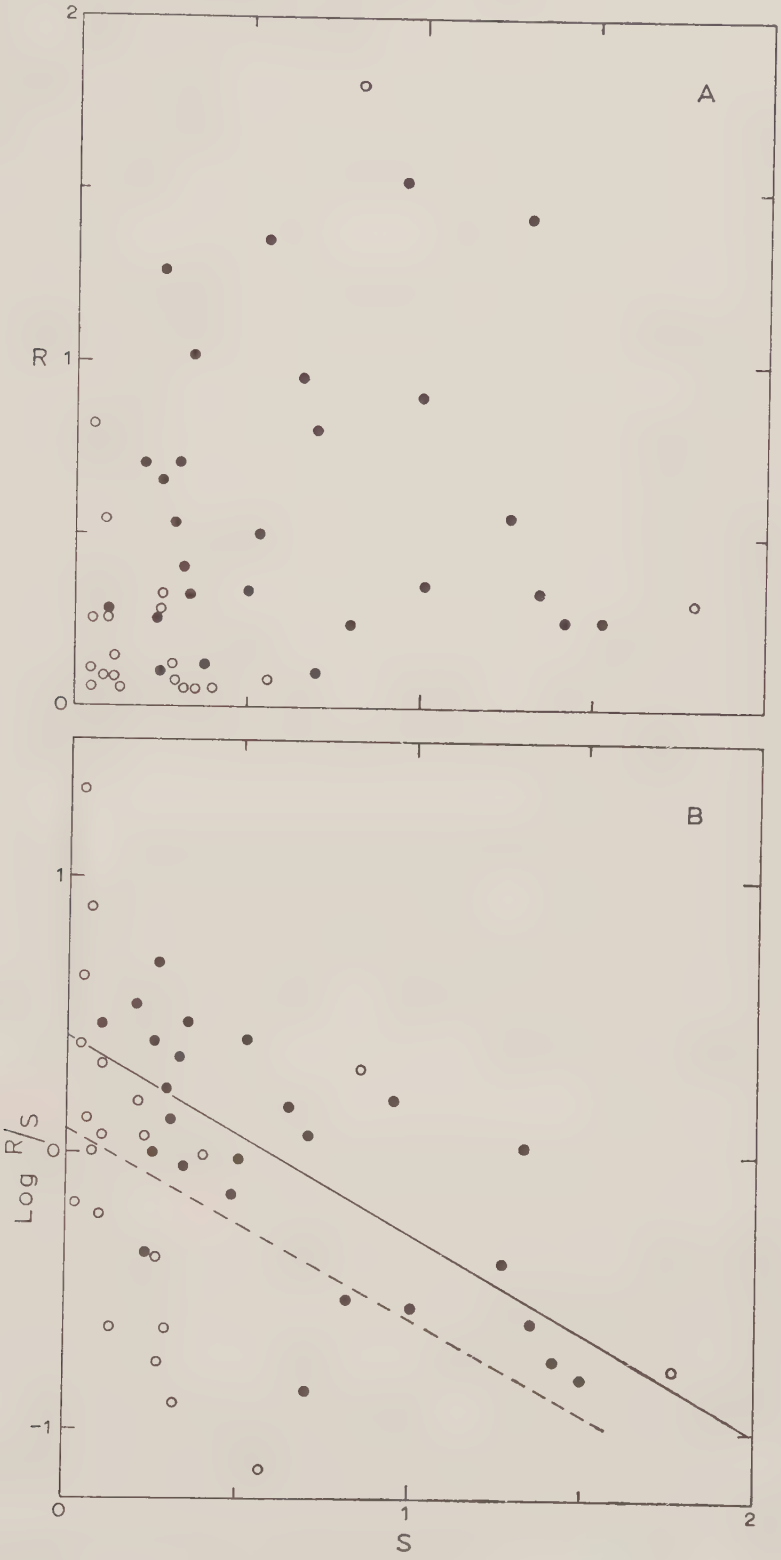

Fig. 18. A. *The relation between recruitment and parent stock for the Sakhalin herring (Ayushin, 1963), for two periods, 1905–29 (open circles) and 1930–54 (solid circles).*
B. *The negative regressions of log R/S on S for the two periods.*

range of stock there is perhaps no dependence of recruitment on parent stock, the state being the asymptotic one of Figure 8.

The same technique can be applied to the year-classes of the Norwegian herring given by Marty and Fedorov (1963). Stock is given as eggs and recruitment as numbers of fish. A fecundity of 70 000 has been taken (from Marty and Fedorov, 1963). Figure 19A shows the relation between recruitment and parent stock in three periods, 1907–29, 1930–42 and 1943–53. Figure 19B gives the relation between log R/S on S for the same three periods.

In the treatment both of the Sakhalin herring and of the Norwegian herring it is likely that F/Z is roughly the same (from the mean ages given by Ayushin, and from the mortalities given by Østvedt, 1963, and by Dragesund and Jakobsson, 1963). Hence the year-class estimates as virtual populations (using Derzhavin's method, 1922) are probably quite reliable. The splitting into separate periods was done using the plot of log R/S on S. The only obvious point that can be made is that as stock increases so the survival of recruits decreases, within each period. In the case of the Sakhalin herring, in the two periods the data are fitted by the same slope; in the case of the Norwegian, in each of the three periods the slopes are different, implying changes in survival rate between periods.

The conclusion from the examination of the Sakhalin and Norwegian herring is very valuable, in that stock and recruitment relations are revealed which are quite like those in other fish populations (Ricker, 1954; Beverton and Holt, 1957; Rounsefell, 1958). Taylor (1963) has shown the same sort of thing for *Clupea pallasii* in British Columbian waters. Within a wide range of stock variation, recruitment is maintained at a steady level, independently of the stock variation. At low levels of stock, recruitment is relatively high and at high levels of stock it is relatively low, and in quantity it is always about the same. This state is presumably achieved by a density-dependent mortality operating somewhere between the egg and the time of recruitment.

It appears that the present stock and recruitment relation for the North Sea Downs stock is a special one, consequent upon its dependence on three-year-old fish. We do not know whether the other North Sea spawning stocks might be exposed to the same danger. The cure is, on the face of it, easy – to reduce fishing effort to such a degree as to allow enough five-year-old fish to live in the stock. If only the Downs stock is affected, because of the special conditions for larval survival in the Southern Bight, then the restriction of fishing effort would have to take into account the mixing of Downs fish in the northern and central North Sea. If all three stocks are potentially affected, then a general restriction of effort would be needed.

SUMMARY

Since 1955, East Anglian driftermen have become more efficient. When this increase in efficiency is taken into account, recruitment to the Downs stock is shown to have declined by nearly three times since the war. The decline is shown in stock, in virtual populations and in stock density.

A stock and recruitment relation is not shown in estimates of stock, but is shown in estimates of stock density. Estimates of larval abundance provide good estimates of stock, and the best demonstration of the stock and recruitment relation is given in relating recruitment (in stock or in density) to larval abundance. As stock has been reduced to a single year-class of three-year-old fish, the percentage mortality from egg to larva has increased by up to four times.

The decline in Downs recruitment could be caused by (*a*) the Bløden fishery for immature herring, (b) a natural change associated with those observed in growth and recruitment, (*c*) as a consequence of the decline in stock through fishing. From discussion of the three possible causes, it is concluded that the decline in recruitment is due to fishing.

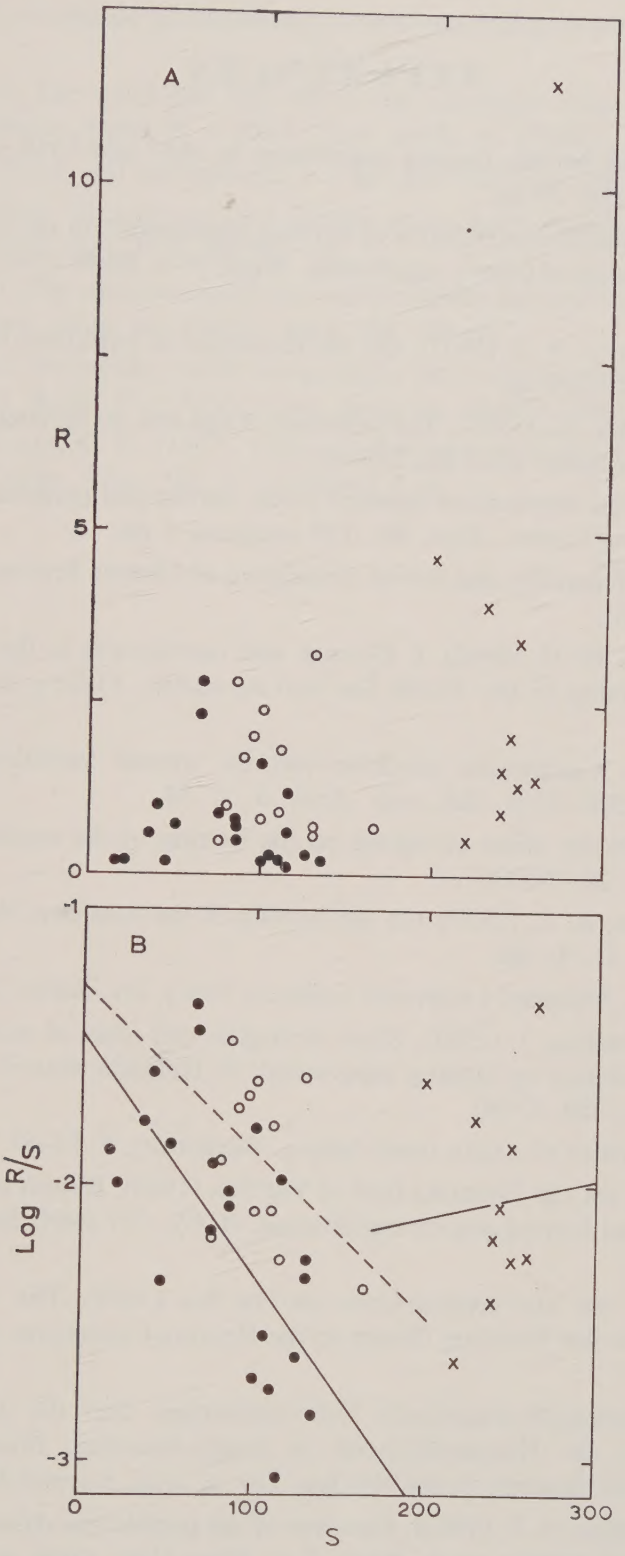

Fig. 19. A. *The relation between recruitment and parent stock for the Norwegian herring* (*Marty and Fedorov*, 1963), *for three periods:* 1907–29 (*solid circles*), 1930–42 (*open circles*) *and* 1943–53 (*crosses*).
B. *The regressions of log R/S on S for the three periods.*

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